

Library
NOAA, National Marine Fisheries Service
SWFC Honolulu Laboratory F/SWC2
2570 Dole Street
Honolulu, HI 96822-2396



Digitized by the Internet Archive
in 2025

**NATIONAL MARINE FISHERIES SERVICE
SOUTHWEST FISHERIES SCIENCE CENTER**

COLLECTED REPRINTS

1987

VOLUME II

M: 8748

Z: 8784

FEBRUARY 1992

TABLE OF CONTENTS

MENDELSSOHN ROY AND JAIME MENDO.

1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, 294-306 p. *In*: D. Pauly and I. Tsukayama (eds.), The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft fur Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines. 8748

MENDELSSOHN, R. AND P. CURY.

1987. Fluctuations of a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions. *Can. J. Fish. Aquat. Sci.* 44:408-421. 8749

MOFFITT, ROBERT B. AND JEFFREY J. POLOVINA.

1987. Distribution and yield of the deepwater shrimp *Heterocarpus* resource in the Marianas. *Fish. Bull., U.S.* 85:339-349. 8750

MOKSNESS, ERLEND, JOHN BUTTLER, AND RICHARD L. RADTKE.

1987. Estimation of age and growth rate in Norwegian spring spawning herring (*Clupea harengus* L.) larvae and juveniles. *Sarsia* 72:341-342. Bergen. ISSN 0036-4827. 8751

MOON, T. W., R. W. BRILL, P. W. HOCHACHKA, AND J.-M. WEBER.

1987. L-(+)-Lactate translocation into the red blood cells of the skipjack tuna (*Katsuwonus pelamis*). *Can. J. Zool.* 65:2570-2573. 8752

MOSER, H. GEOFFREY AND JOHN L. BUTLER.

1987. Descriptions of reared larvae of six species of *Sebastes*. *In*: W. H. Lenarz and D. R. Gunderson (eds.), Widow rockfish. Proceedings of a workshop, Tiburon, California, December 11-12, 1980, p. 19-29. NOAA Tech. Rep. NMFS-48. 8753

MOSER, H. GEOFFREY, PAUL E. SMITH, AND LAWRENCE E. EBER.

1987. Larval fish assemblages in the California Current region, 1954-1960, a period of dynamic environmental change. *Calif. Coop. Oceanic Fish. Invest. Rep.* 28:97-127. 8754

TABLE OF CONTENTS (CONTINUED)

MUNDY, B. C.

1987. NMFS, Southwest Fisheries Center, Honolulu Laboratory, Honolulu, Hawaii: Insular Resources Investigation. Early Life History Section, Am. Fish. Soc. Newsl. 8(1):12-13. 8755

MURANO, MASA AKI AND JAMES R. CHESSE.

1987. Four new mysids from California coastal waters. J. Crust. Biol. 7(1):182-197. 8756

NORTON, JERROLD.

1987. Ocean climate influences on groundfish recruitment in the California Current. Proc. Int. Rockfish Symp., Oct. 20-22, 1986, Anchorage, Alaska. Alaska Sea Grant Rep. 87-2, Univ. of Alaska, p. 73-98. 8757

PERRIN, W. F., E. D. MITCHELL, J. G. MEAD, D. K. CALDWELL, M. C. CALDWELL, P. J. H. van BREE, AND W. H. DAWBIN.

1987. Revision of the spotted dolphins, *Stenella* spp. Mar. Mammal Sci. 3(2):99-170. 8758

PITMAN, ROBERT L., ANELIO AGUAYO L., AND JORGE URBAN R.

1987. Observations of an unidentified beaked whale (*Mesoplodon* sp.) in the eastern tropical Pacific. Mar. Mammal Sci. 3(4):345-352. 8759

POLACHECK, T.

1987. Relative abundance, distribution and inter-specific relationship of cetacean schools in the eastern tropical Pacific. Mar. Mammal Sci. 3(1):54-77. 8760

POLOVINA, JEFFREY J.

1987. Assessment and management of deepwater bottom fishes in Hawaii and the Marianas. In: Jeffrey J. Polovina and Stephen Ralston (eds.), Tropical snappers and groupers: Biology and fisheries management, p. 505-532. Westview Press, Boulder and London. 8761

POOLEY, SAMUEL G.

1987. Demand considerations in fisheries management--Hawaii's market for bottomfish. In: Jeffrey J. Polovina and Stephen Ralston (eds.), Tropical snappers and groupers: Biology and fisheries management, p. 605-638. Westview Press, Boulder and London. 8762

TABLE OF CONTENTS (CONTINUED)

RALSTON, STEPHEN

1987. Mortality rates of snappers and groupers. *In*: Jeffrey J. Polovina and Stephen Ralston (eds.), *Tropical snappers and groupers: Biology and fisheries management*, p. 375-404. Westview Press, Boulder and London. 8763

REILLY, S. B.

1987. Reanalysis of rate of change in the California-chukotka gray whale stock, 1967/68-1979/80. *Rep. Int. Whal. Commn* 37:347-349. 8764

SAKAGAWA, GARY T., ATILIO L. COAN, AND NORMAN W. BAR-TOO.

1987. Patterns in longline fishery data and catches of bigeye tuna, *Thunnus obesus*. *Mar. Fish. Rev.* 49(4):57-66. 8765

SHOMURA, RICHARD S.

1987. Tuna tagging in the Philippines, Thailand, and Malaysian waters. *In*: Report of the Second Meeting of the Tuna Research Groups in the Southeast Asian Region, Manila, Philippines, August 25-28, 1987, pp. 63-74 [original pagination]. Indo-Pacific Tuna Development and Management Programme, IPTP/87/GEN/12. 8766

SQUIRE, JAMES L.

1987. Pacific billfish angler catch rates for key area stock assessments. *Mar. Fish. Rev.* 49(2):15- 25. 8767

SQUIRE, JAMES L.

1987. Relation of sea surface temperature changes during the 1983 El Niño to the geographical distribution of some important recreational pelagic species and their catch temperature parameters. *Mar. Fish. Rev.* 49(2):44-57. 8768

SQUIRE, JAMES L.

1987. Striped marlin, *Tetrapturus audax*, migration patterns and rates in the northeast Pacific Ocean as determined by a cooperative tagging program: its relation to resource management. *Mar. Fish. Rev.* 49(2):26- 43. 8769

TABLE OF CONTENTS (CONTINUED)

SQUIRES, DALE

1987. Fishing effort: Its testing, specification, and internal structure in fisheries economics and management. *J. Environ. Econ. Manage.* 14:268-282. 8770

SQUIRES, DALE

1987. Long-run profit functions for multiproduct firms. *Amer. J. Agr. Econ.* 69(3):558-569. 8771

SQUIRES, DALE

1987. Public regulation and the structure of production in multiproduct industries: an application to the New England otter trawl industry. *Rand J. Econ.* 18(2):232-247. 8772

TAYLOR, M. K., D. P. DEMASTER, F. L. BURNELL, AND R. E. SCHWEINSBURG.

1987. Modeling the sustainable harvest of female polar bears. *J. Wildl. Manage.* 51(4):811-820. 8773

THEILACKER, GAIL H.

1987. Feeding ecology and growth energetics of larval northern anchovy, *Engraulis mordax*. *Fish. Bull., U.S.* 85(2):213-228. 8774

UEBER, EDWARD.

1987. Widow rockfish fishery. *In:* William H. Lenarz and Donald R. Gunderson (eds.), *Widow rockfish*. 53- 56. Proceedings of a workshop, Tiburon, California, December 11-12, 1980, p. 53-56. NOAA Tech. Rep. NMFS-48. 8775

WAHLEN, BRUCE E., RUTH B. MILLER, AND CAROLYN J. MACKY.

1987. Composition of the incidental kill of small cetaceans in the US purse-seine fishery for tuna in the eastern tropical Pacific during 1985. *Rep. Int. Whal. Commn* 37:353-355. 8776

WETHERALL, J. A., J. J. POLOVINA, AND S. RALSTON.

1987. Estimating growth and mortality in steady-state fish stocks from length-frequency data. *In:* D. Pauly and G. R. Morgan (eds.), *Length-based methods in fisheries research*, p. 53-74. International Center for Living Aquatic Resource Management, ICLARM Conference Proceedings 13, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait. 8777

TABLE OF CONTENTS (CONTINUED)

WHIPPLE, J. A., R. B. MacFARLANE, M. B. ELDRIDGE, AND
P. BENVILLE, JR.

1987. The impacts of estuarine degradation and chronic pollution on populations of anadromous striped bass (*Morone saxatilis*) in the San Francisco Bay-Delta, California: A summary. In: D. M. Goodrich (ed.), San Francisco Bay: Issues, resources, status, and management, p. 77-106. NOAA Estuary-of-the-Month Seminar Series No. 6. U.S. Dep. Commer., NOAA Estuarine Programs Office. 8778

WILLIAMS, G., M. A. CRAWFORD, AND W. F. PERRIN.

1987. Comparison of the fatty acid component in structural lipids from dolphins, zebra and giraffe: possible evolutionary implications. J. Zool., Lond. 213:673-684. 8779

WOLF, PATRICIA, PAUL E. SMITH, AND CHERYL L. SCANNELL.

1987. The relative magnitude of the 1986 Pacific sardine spawning biomass off California. Calif. Coop. Oceanic Fish. Invest. Rep. 28:21-26. 8780

WYLLIE ECHEVERRIA, TINA.

1987. Relationship of otolith length to total length in rockfishes from northern and central California. Fish. Bull., U.S. 85(2):383-387. 8781

WYLLIE ECHEVERRIA, TINA

1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. Fish. Bull., U.S. 85(2):229-250. 8782

YOCHAM, P. K., B. S. STEWART, R. L. DELONG, AND D. P.
DEMASTER.

1987. Diel haul-out patterns and site fidelity of harbor seals (*Phoca vitulina*) on San Miguel Island, CA, in autumn. Mar. Mammal Sci. 3(4):323-332. 8783

YOKLAVICH, M. M. AND G. W. BOEHLERT.

1987. Daily growth increments in otoliths of juvenile black rockfish, *Sebastes melanops*: an evaluation of autoradiography as a new method of validation. Fish. Bull., U.S. 85(4):826-832. 8784

TABLE OF CONTENTS (CONTINUED)

The following publications are not included in the Collected Reprints for 1987:

ALVARIÑO, ANGELES AND CAROL A. KIMBRELL.

1987. Abundance of zooplankton species in California coastal waters during April 1981, February 1982, March 1984 and March 1985. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-74, 59 p.

AMBROSE, DAVID A., RICHARD L. CHARTER, H. GEOFFREY MOSER, AND CELESTE R. SANTOS METHOT.

1987. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1955. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-83, 185 p.

AMBROSE, DAVID A., RICHARD L. CHARTER, H. GEOFFREY MOSER, AND CELESTE R. SANTOS METHOT.

1987. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1960. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-88, 253 p.

BALAZS, GEORGE H., ROBERT G. FORSYTH, AND ALAN K. H. KAM.

1987. Preliminary assessment of habitat utilization by Hawaiian green turtles in their resident foraging pastures. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-71, 107 p.

BOGGS, C. H. AND S. G. POOLEY.

1987. Forces of change in Hawaii's aku (skipjack tuna) industry, 1986 - workshop summary. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-72, 71 p.

GILPATRICK, J. W., W. F. PERRIN, S. LEATHERWOOD, AND L. SHIROMA.

1987. Summary of distribution records of the spinner dolphin, *Stenella longirostris*, and the pantropical spotted dolphin, *S. attenuata*, from the western Pacific Ocean, Indian Ocean and Red Sea. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-89, 42 p.

TABLE OF CONTENTS (CONTINUED)

HARRISON, JOHN T.

1987. The 40 MW_e OTEC plant at Kahe Point, Oahu, Hawaii: A case study of potential. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-68, 105 p.

HOLT, RENNIE S. AND ALAN JACKSON.

1987. Report of a marine mammal survey of the eastern tropical Pacific aboard the research vessel *McArthur*, July 29-December 6, 1986. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-77, 161 p.

HOLT, RENNIE S. AND STEPHANIE N. SEXTON.

1987. Report of a marine mammal survey of the eastern tropical Pacific aboard the research vessel *David Starr Jordan*, July 29-December 5, 1986. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-76, 171 p.

JOHANOS, THEA C., ALAN K. H. KAM, AND ROBERT G. FORSYTH

1987. The Hawaiian monk seal on Laysan Island: 1984. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-70, 38 p.

KEATING, BARBARA H., PATRICIA FRYER, RODEY BATIZA, AND GEORGE W. BOEHLERT. (EDS.).

1987. Seamounts, islands, and atolls. Geophys. Monogr. 43, 405 p. [Am. Geophys. Union.]

MAJORS, ANTHONY P.

1987. United States North Pacific albacore fishery, 1961-1980, Vol. 1. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-73, 11 p.

OWEN, R. W. AND CAROL A. KIMBRELL.

1987. Micropatch sampler data. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-91, 54 p.

POLOVINA, JEFFREY J. AND STEPHEN RALSTON (EDS.).

1987. Tropical snappers and groupers: Biology and fisheries management. Westview Press, Boulder and London, 659 p.

TABLE OF CONTENTS (CONTINUED)

POMMERANZ, TILMAN AND H. GEOFFREY MOSER.

1987. Data report on the vertical distribution of the eggs and larvae of northern anchovy, *Engraulis mordax*, at two stations in the Southern California Bight. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-75, 9 p.

SAKAGAWA, GARY T.

1987. Effects of tropical tuna fisheries on non-target species. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-69, 29 p.

SANDKNOP, ELAINE M., RICHARD L. CHARTER, H. GEOFFREY MOSER, AND CELESTE R. SANTOS METHOT.

1987. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1952. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-80, 207 p.

SANDKNOP, ELAINE M., RICHARD L. CHARTER, H. GEOFFREY MOSER, AND CELESTE R. SANTOS METHOT.

1987. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1958. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-86, 248 p.

STEVENS, ELIZABETH G., RICHARD L. CHARTER, H. GEOFFREY MOSER, AND MORGAN S. BUSBY.

1987. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1953. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-81, 186 p.

STEVENS, ELIZABETH G., RICHARD L. CHARTER, H. GEOFFREY MOSER, AND MORGAN S. BUSBY.

1987. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1956. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-84, 189 p.

STEVENS, ELIZABETH G., RICHARD L. CHARTER, H. GEOFFREY MOSER, AND MORGAN S. BUSBY.

1987. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1959. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-87, 273 p.

TABLE OF CONTENTS (CONTINUED)

SUMIDA, BARBARA Y., RICHARD L. CHARTER, H. GEOFFREY MOSER, AND DEBORAH L. SNOW.

1987. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1954. U.S. Dep. Commer., NOAA Tech Memo., NOAA-TM-NMFS-SWFC-82, 207 p.

SUMIDA, BARBARA Y., RICHARD L. CHARTER, H. GEOFFREY MOSER, AND DEBORAH L. SNOW.

1987. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1957. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-85, 225 p.

THAYER, V. G., S. B. REILLY, P. C. FIEDLER, C. W. OLIVER, AND D. W. BEHRINGER.

1987. Report of ecosystem studies conducted during the 1987 eastern tropical Pacific dolphin survey on the research vessel *McArthur*. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-104, 112 p.

THAYER, V. G., R. L. PITMAN, K. A. RITTMASER, G. G. THOMAS, D. W. BEHRINGER, AND S. B. REILLY.

1987. Report of ecosystem studies conducted during the 1986 eastern tropical Pacific dolphin survey on the research vessel *David Starr Jordan*. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-105, 106 p.

THOMSON, CYNTHIA J. AND DANIEL D. HUPPERT.

1987. Results of the Bay area sportfish economic study (BASES). U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-78, 29 p.

WILSON, C. E., W. F. PERRIN, J. W. GILPATRICK, JR., AND S. LEATHERWOOD.

1987. Summary of locality records of the striped dolphin, *Stenella coeruleoalba*. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-90. 27 p. survey cruises in 1953. U.S. Dep. Commer., NOAA Tech. Memo., NOAA-TM-NMFS-SWFC-81, 186 p.

Exploratory Analysis of Anchoveta Recruitment off Peru and Related Environmental Series *

ROY MENDELSON

*Pacific Fisheries Environment Group
Southwest Fisheries Center
P.O. Box 831
Monterey, California 93942
USA*

JAIME MENDO

*Instituto del Mar del Peru
Apartado 22, Callao, Peru*

MENDELSON, R. and J. MENDO. 1987. Exploratory analysis of anchoveta recruitment off Peru and related environmental series, p. 294-306. In D. Pauly and L. Tsukayama (eds.) The Peruvian anchoveta and its upwelling ecosystem: three decades of change. ICLARM Studies and Reviews 15, 351 p. Instituto del Mar del Peru (IMARPE), Callao, Peru; Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), GmbH, Eschborn, Federal Republic of Germany; and International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines.

Abstract

An exploratory analysis of monthly anchoveta (*Engraulis ringens*) recruitment estimates and associated biological and environmental series for the years 1953 to 1981 was performed with the aim of investigating the possibility of forecasting anchoveta recruitment three months ahead of time. While the high degree of autocorrelation in the monthly recruitment series prevented the identification of causal models, yearly models combining pairs of adjacent months were identified which appear promising as a means to forecast future trends in anchoveta recruitment. These models, however, do not appear to conform to any of the conventional hypotheses providing mechanisms to explain recruitment fluctuations.

Introduction

Recruitment is one of the most important but least understood components of fish population dynamics. Several authors have tried to empirically relate larval survivorship with environmental parameters (Bailey 1981; Lasker 1981). These efforts to relate recruitment variability with environmental variability have not been notably successful due to the very short data series generally available for empirical analysis (Bakun 1986). Major recent studies have indicated environmental-biological linkages for pelagic and demersal species of the California Current, Canary Current and Guinea Current (see Bakun 1986). Wind induced Ekman transport, a turbulent mixing index (wind speed cubed) and temperature also have been used in several studies of environmental effects on fish stocks (e.g., Collins and MacCall 1977; MacCall 1980; Bakun and Parrish 1980; Mendelsohn and Cury 1987).

Similar studies have yet to be done for the Peruvian anchoveta (*Engraulis ringens*) which in the early 1970s generated the highest catch of any single-species fishery in the world (Tsukayama and Palomares, this vol.; Castillo and Mendo, this vol.), and whose biomass was well over 20 t x 10⁶ by the end of the 1960s (Pauly, Palomares and Gayanilo, this vol.). The collapse of the anchoveta fishery has been attributed both to overfishing and to the influence of El Niño which may have changed the usual spawning patterns of the anchoveta (Santander 1980).

*PROCOPA Contribution No. 53.

The biology of the anchoveta is rather well documented (see relevant contributions in this vol.). Spawning in anchoveta tends to have two peaks per year - one in the austral winter-spring and the other in austral summer. The major spawning concentrations usually occur near the coast up to around 105 km offshore. Since the 1960s, the Instituto del Mar del Peru (IMARPE) has carried out anchoveta egg and larval surveys (see Santander, this vol.), but these data do not necessarily indicate variations in anchoveta recruitment due to density-dependent egg cannibalism, other sources of egg mortality and fluctuations in survival of the larvae (see Pauly, this vol.).

Several authors (Santander 1980; Mendiola and Ochoa 1980; Tsukayama and Alvarez 1980; Santander and Flores 1983) have presented evidence showing that during El Niño years, primary productivity decreased and the periods of peak spawning changed resulting in lower recruitment. These two factors have been thought to be the major environmental influences on recruitment variability.

In this paper we perform an exploratory data analysis of the estimated recruitment and biomass series of Pauly, Palomares and Gayanilo (this vol.), of the egg production series in Pauly and Soriano (this vol.) and of several of the various environmental series gathered in this volume. Our interest is in determining if it is possible to forecast anchoveta recruitment at least three months ahead of time, a forecast that would be useful in managing the fishery.

Exploratory data analysis has the advantage in this situation where little is known in that we do not try to force the data into models that may not agree with the structure of the observed data. Despite the variety of fisheries models available, there is no "physics of fisheries" in the sense of known laws that have been experimentally verified. Letting the data lead us to a model structure leaves us open to alternative causal explanations as well as providing a check on the realism of the estimated series, identifying outliers in the data and flagging data points that may be overly influential in the analysis.

The Data

The anchoveta population data used are the estimates presented by Pauly, Palomares and Gayanilo (this vol.). The environmental series consisted of sea surface temperature (SST) and oceanic wind speed cubed and offshore transport derived by Bakun (this vol.), as well as hourly wind direction and intensity recorded at Trujillo and Callao airports by CORPAC (Corporacion Peruana de Aviacion Comercial). The Trujillo and Callao data are described further in Mendo et al. (1987) and Mendo et al. (this vol.).

Offshore transport at both Trujillo and Callao were calculated as in Bakun (1973 and this vol.), as was wind speed cubed for both locations. Peterman and Bradford (1987) report using an index reflecting Lasker's hypothesis (1978) to predict the survival of anchovy *Engraulis mordax* larvae off California. A similar index was computed for both Trujillo and Callao; it measures the number of 4-day periods during which the wind speed did not exceed 5 m/sec. These 4-day periods are here called "Lasker events", as suggested by D. Pauly (pers. comm.).

Spectral analysis showed that the Trujillo and Callao wind series were not significantly coherent at all frequencies. The Trujillo wind series were only coherent with the oceanic wind series at a frequency of 6 months (though out of phase) and at frequencies longer than a year. The oceanic series show a pronounced seasonal cycle, the Callao series a smaller seasonal cycle and the Trujillo series showed essentially no seasonal cycle. The general impression is of strong local differences suggesting the need for care in choosing what variables to use in the analysis.

The Lasker events were problematic at best. At Callao, the wind always satisfied the criteria, while at Trujillo most months had a zero incidence of the necessary periods of calm, especially during 1955-1970, when recruitment was at high levels (see below and Table 1). The estimated recruitment following the periods of zero counts vary greatly, making Lasker events of little use for these periods. For the periods where numerous Lasker events occurred, examination of the data revealed that a high number of events tended to precede low rather than high recruitment. Lasker's hypothesis is based on experience in California where turbulence disperses the food necessary for larval survival; in Peru the food concentration in the mixed layer may be

high enough for turbulence not to have that great an effect. All that can be said with certainty from this is that the situation in Peru appears to differ from that in California.

Table 1. Monthly occurrence of "Lasker events" near Trujillo, 1953-1985.^a

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1953	0	7	2	0	0	1	6	19	2	2	0	0
1954	0	6	20	0	0	0	0	0	0	0	0	0
1955	0	0	0	0	0	0	0	0	0	0	0	0
1956	0	0	0	0	0	0	0	0	0	0	0	0
1957	0	0	0	0	0	0	0	0	0	0	0	0
1958	0	0	0	0	0	0	0	0	0	0	0	0
1959	0	1	0	0	0	0	0	0	0	0	0	0
1960	0	0	0	0	0	0	0	0	0	0	0	0
1961	1	3	2	0	0	0	0	0	0	0	0	0
1962	0	0	0	0	0	0	2	0	0	0	0	0
1963	0	1	0	0	0	2	1	0	0	0	0	0
1964	0	0	0	0	0	3	0	0	0	0	0	2
1965	3	0	1	0	0	0	0	0	0	0	0	0
1966	0	0	0	0	0	0	0	0	0	0	0	0
1967	0	0	0	0	0	0	0	0	0	0	0	0
1968	0	0	0	0	0	0	0	0	0	0	0	0
1969	0	0	0	0	0	0	4	0	1	0	0	0
1970	0	0	0	0	0	0	0	0	0	0	0	0
1971	0	2	8	0	0	0	3	0	0	0	0	0
1972	2	1	0	0	0	0	0	0	0	0	0	0
1973	0	0	0	0	0	0	0	0	0	0	0	1
1974	20	27	22	6	3	0	6	5	0	0	0	0
1975	3	6	4	1	0	0	0	0	0	0	0	0
1976	0	1	0	0	0	0	0	0	0	0	0	1
1977	0	0	0	0	1	0	3	0	0	0	4	0
1978	0	0	0	0	12	4	3	3	0	4	11	1
1979	0	0	7	6	2	8	7	2	0	0	0	1
1980	0	0	1	0	0	0	0	0	0	0	0	0
1981	0	2	5	0	5	10	8	1	1	0	1	6
1982	14	12	6	1	21	30	30	31	30	31	30	5
1983	0	0	12	12	4	0	7	0	0	0	0	0
1984	3	1	0	0	0	1	17	3	0	0	2	1
1985	6	1	2	6	2	0	0	2	0	0	0	0

^aBased on data in Mendo et al. (1987); a "Lasker event" is a period of calm (wind speed below 5 m/s) lasting 4 days; periods of 5 days are viewed as two partly overlapping 4-day events, etc. (see Peterman and Bradford 1987, note 16).

Based on this preliminary analysis of the environmental series, we restricted our attention to the wind variables at Trujillo. The Trujillo station has no nearby topographic interference, such as mountains, and the coastline from one degree north of Trujillo to one degree south of Trujillo is almost straight. The area off Trujillo also is one of the major anchoveta spawning areas (Santander and Castillo 1973; Santander 1980, this vol.).

Localized trends were calculated using the "lowess" algorithm of Cleveland (1979) for recruitment, egg and total biomass as well as for offshore transport and wind speed cubed at Trujillo. Both the recruitment and total biomass series exhibit three periods with distinct mean levels. A pre-1960 period with low levels of biomass and recruitment, a period from 1960 to 1972 when both biomass and recruitment were at high levels, and a post-1972 period following the collapse of the fishery (see Pauly, Palomares and Gayanilo, this vol.). On a log scale, for the 1960-1972 period, the trend line for both recruitment and total biomass is almost flat, suggesting random variation around a fixed mean level.

Recruitment Series

For our initial look at anchoveta recruitment we examined the dynamics of the recruitment series by decomposing it into three components - localized trend, seasonal and autoregressive (AR) components (Fig. 1), using an algorithm of Gersch and Kitigawa (1983). The variation in recruitment is dominated by longer-term behavior captured in the estimated trend, as the AR component is an order of magnitude smaller than the recruitment series and the seasonal component is almost two orders of magnitude smaller.

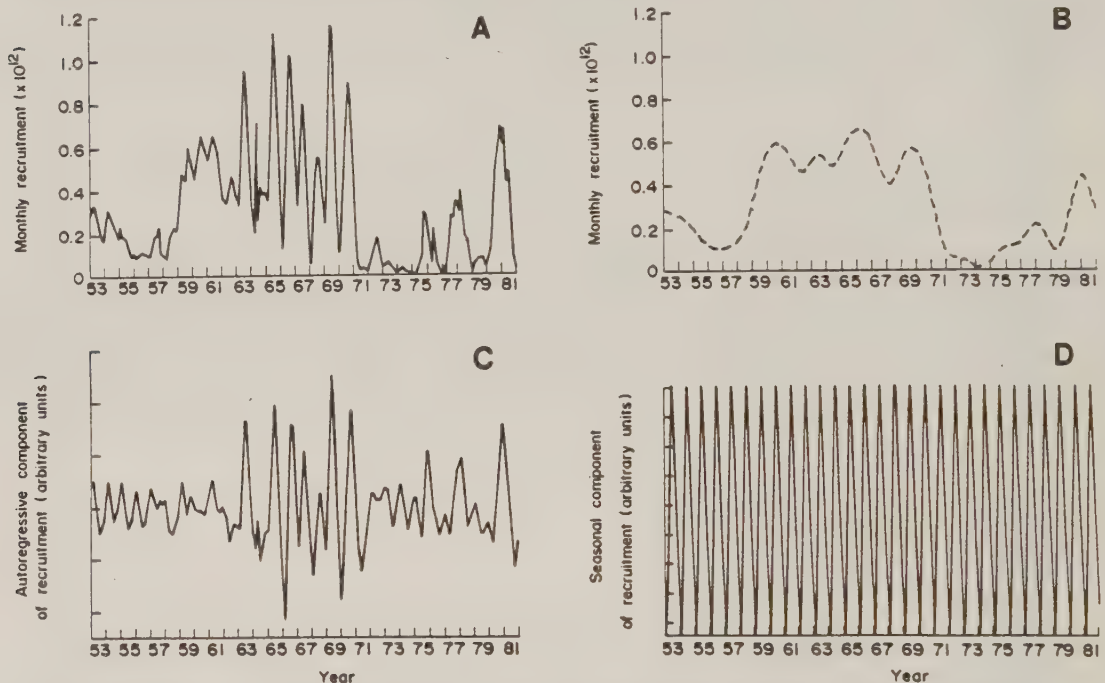


Fig. 1. Decomposition of the anchoveta recruitment time series into its component parts: (A) observed data; (B) estimated trend; (C) autoregressive component; (D) seasonal component (see text for details).

The estimated local trend (Fig. 1B) suggests three different periods: a low level of recruitment from 1953 to 1958, a higher level from 1959 to 1969 or 1970, followed by a sharp drop in recruitment which preceded: (i) the El Niño even to 1972-1973, (ii) the collapse of the fishery, (iii) and by a year, the drop in total biomass. This suggests that the effects of El Niños on the population dynamics of anchoveta may be more complex than previously thought. The 1971 recruitment collapse must have been due to overfishing or environmental effects the previous years since the collapse of the fishery appears to have begun before the El Niño.

The seasonal component (Fig. 1D) is very regular but of such small magnitude as to be almost unnoticeable in the overall variation in recruitment. The autoregressive component (Fig. 1C) also suggests three periods: a period from 1953 to 1961 of relatively small variations, a period from 1961 to 1972 of large variations coinciding with the growth of a large-scale fishery and a period from 1972 or so onwards following the collapse of the fishery which is also a period of smaller variations in recruitment. The period of high variability from 1961 to 1972 also is a period of high estimated total biomass.

The autocorrelation function of recruitment both on the normal and the log scale is highly nonstationary and dominated by a value of .95 at a lag of one month. A simple model that includes an autoregressive term of recruitment on itself at lags 1, 2, 6 and 12 months explains almost 96% of the variance in the monthly series. This agrees with the decomposition of the time

series: monthly estimates of recruitment have not increased our degrees of freedom as the series is not independent at monthly time spans; rather, the important variation is between years.

The high degree of autocorrelation in the monthly recruitment series is probably caused by (i) the fact that the sampled length-frequency data may not be accurate enough to resolve monthly differences in population structure so that the size information tends to be "smeared" across months, (ii) the fact that Virtual Population Analysis (VPA) uses a series of recursive equations that estimate the present biomass levels from the data from successive periods; these equations will tend to smooth the observed data towards low-order autoregressive behavior, reducing the independence of the monthly data and (iii) the fact that the version of length-structured VPA used by Pauly, Palomares and Gayanilo (this vol.) increases the inherent tendency of VPA to smooth data across months (D. Pauly, pers. comm.).

There are several approaches for analyzing the recruitment series given this high degree of autocorrelation. We can low-pass filter the series and then decimate the results to one or two representative values a year and use these data points as the new time series. Alternatively, we can form separate annual series of seasonal segments of the annual cycle and fit separate models across years for each of the aggregate series, comparing the results of the different models. This second approach has an added advantage that it allows us to check for time-dependent relationships in the data. In what follows we restrict ourselves to this second approach.

Bimonthly Recruitment Series

As an initial examination of the data by months across years, we constructed box plots (Velleman and Hoaglin 1981) for each of the series (Fig. 2). A plus marks the median of the data, the I's mark the hinges plus or minus 1.5 times the H-spread, where the hinges are the medians of the two halves of the series defined by the median and the H-spread is the difference between the two hinges. The lines beyond the boxes show the outer normal range of the data which is defined as the hinges plus or minus 3 times the H-spread. Values somewhat outside this range are marked with dots and values far outside this range with open dots. Finally, the parentheses denote a confidence limit on the medians.

Recruitment (Fig. 2A) starts out in January at a relatively lower level, increases gradually to a recruitment peak around May-July and then slowly decreases to the end of the year. Egg production, however, has a relative peak around February-March and a much larger peak around September-October. Parent biomass (Fig. 2C) has a large peak in February-March concurrent with the relative peak in egg production but usually has relatively low value during the September-October period. Thus assuming the recruits to be 3-4 months old (see Palomares et al., this vol.), the larger recruitment in June-July would stem from the lesser spawning of February-March, which is based on a large parent biomass. Conversely, the lesser recruitment in the beginning of the year would stem from the major spawning in September-October, which is based on a relatively small parent biomass. The wind-related environmental series (Figs. 2E and 2F) are at a relative minimum during the February-March period, but are at their maxima during the September-October period and thus generate unfavorable environmental conditions. Parrish et al. (1984) also comment on the large austral spring spawning during unfavorable conditions. One possible explanation for a large spawning during unfavorable conditions is that the conditions during this period are favorable for the adults (it is the upwelling period). A. Bakun (pers. comm.) has suggested that such a low degree of apparent adaptation of spawning effort to the normal seasonality of larval survival prospects might be in some way due to the fact that detrimental El Niño effects may exert strongest impact during the warm austral summer period; thus the effects of intermittent reproductive failures during summer, associated with El Niño anomalies may have tended to counter adaptive tendencies to concentrate spawning in the normally favorable summer season.

After examination of the recruitment series and the environmental series we decided on bimonthly aggregation of the recruitment series as follows: February-March, April-May, June-July, August-September, October-November and December-January. Note that the December-January aggregate crosses years: December 1953 is combined with January 1954, etc. These pairs of months vary across years in a similar manner and at similar levels (Fig. 3). For

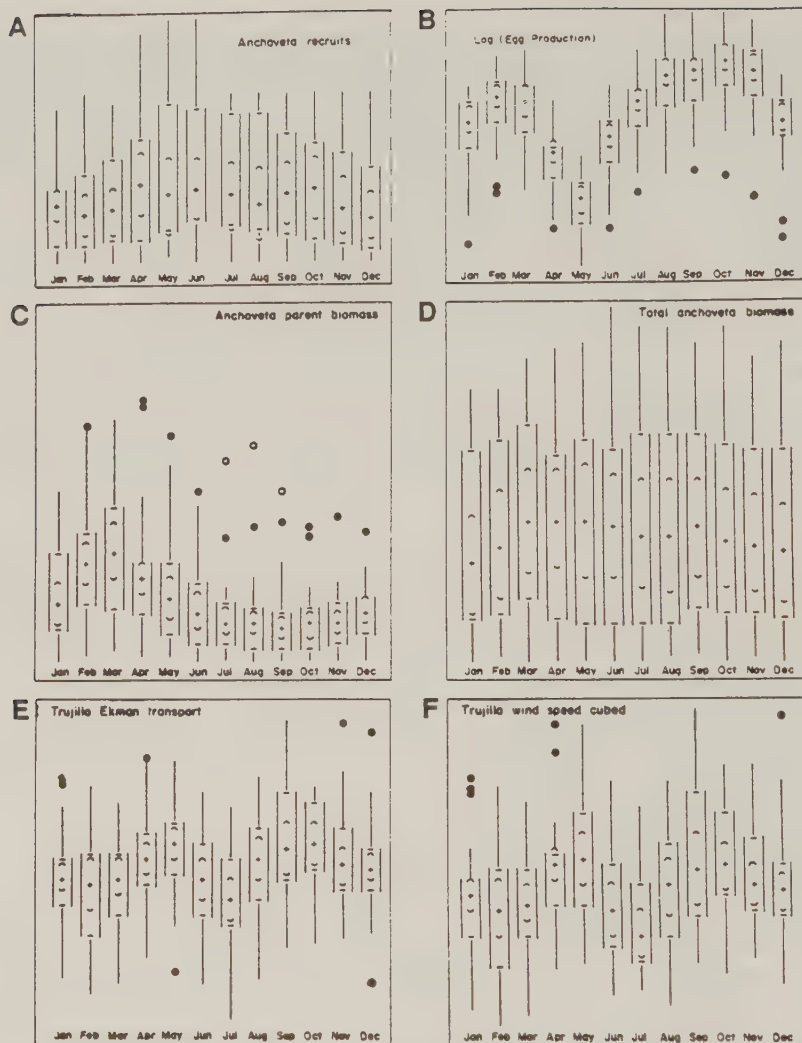


Fig. 2. Boxplots of the monthly anchoveta and wind-based environmental series: (A) recruitment; (B) log of egg production; (C) parent biomass; (D) total biomass; (E) Trujillo offshore transport; (F) Trujillo wind speed cubed (see text for definition of ordinate and data sources).

predictors we considered parent biomass and egg production lagged 3 and 4 months (the spawning period) as well as the monthly offshore transport and wind speed cubed at Trujillo. Spectral analysis of the transport and wind speed cubed at Trujillo shows that these series are highly coherent ($> .9$) at all frequencies and thus have essentially the same dynamics due to limited variability in the wind direction (Mendo et al., this vol.). We therefore arbitrarily restrict our attention to offshore transport, though similar results can be found using wind speed cubed, i.e., turbulence.

Cross-correlation matrices as well as generalized partial correlations were calculated as in Tiao and Box (1982). Model and variable selection were also examined using the multivariate subset autoregression procedure of Akaike et al. (1979). As it is likely that the relationships between recruitment and the environment is nonlinear, final model selection and identification was done using the AVAS procedure (Tibshirani 1987). This procedure is a modification of the optimal transformation algorithm ACE (Breiman and Friedman 1985) which appears to correct

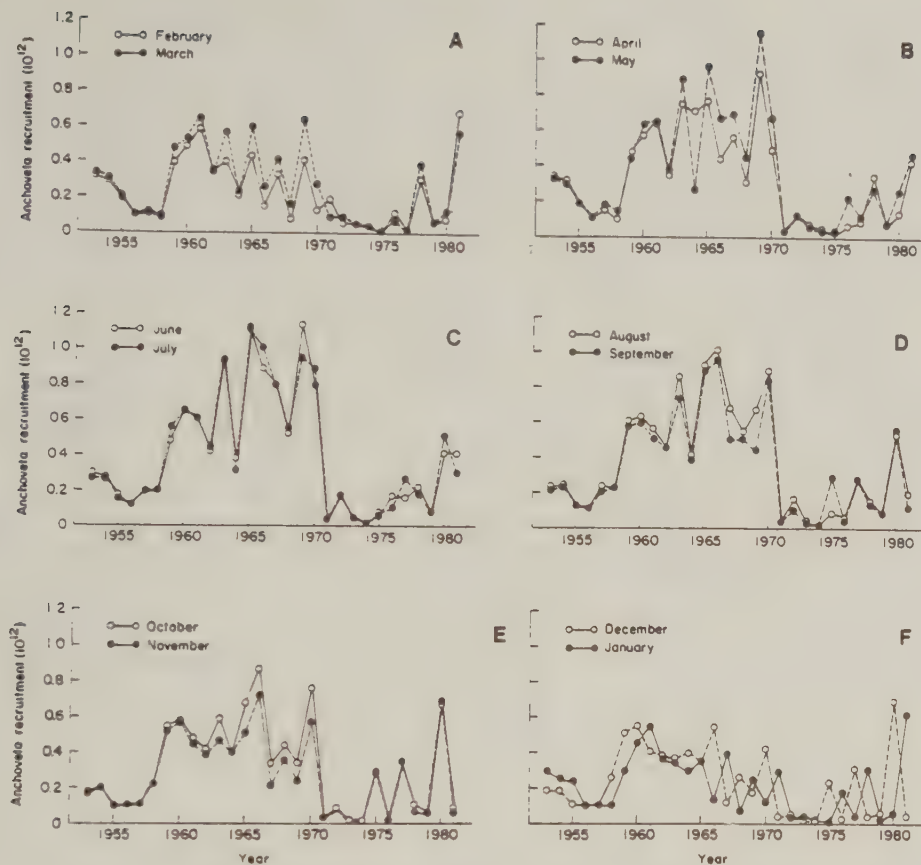


Fig. 3. Monthly anchoveta recruitment across years, 1953 to 1981: (A) February-March; (B) April-May; (C) June-July; (D) August-September; (E) October-November; (F) December-January.

some of the problems with that algorithm, by restricting the transformation of the dependent variable to be monotone and variance stabilizing (Efron 1982).

Both the approach of Tiao and Box (1982) and the subset autoregression procedure suggested the same behavior in all the series. Each of the bimonthly recruitment series had a significant relationship with recruitment two years hence. Parent biomass 3 and 4 months earlier appears to have no significant effect on recruitment. Except in one case to be discussed below, environmental conditions during the spawning period also do not appear to be strongly related to recruitment. Egg production was not examined for all the bimonthly series; however, for the models in which egg production was used as a variable it also was not significantly related to recruitment 3-4 months later.

For all six bimonthly series, offshore transport during the austral spring period September-November was identified as the important predictor of recruitment, and that the strongest relationship appeared to be with September transport. To obtain our models, the AVAS algorithm was used on each of the six bimonthly recruitment series, using recruitment two years earlier and September-November transport as variables. The variables were selected in a stepwise fashion by first identifying the best single variable, then by finding the second variable that when added to best single predictor produces the most increase in r -square value, etc. As a partial check on our procedure, monthly transport series were chosen at random for inclusion in our analysis; at no point did any of these series produce a significant result. Since AVAS produces transformations that can improve the relationship between variables if the relationship is nonlinear, we also tested the inclusion of parent biomass and environmental conditions 3-4

months previous to recruitment. Again, with one exception, none of these series added significantly to our results.

The models estimated by AVAS all had estimated r-square values in the range of .75 to .80. Given the relative short length of our time series as well as the amount of searching we did over variables, it would not surprise us if this value is inflated as a measure of prediction r-square, that is of expected error in forecasting future data rather than the error from the data used to estimate the models (see also Efron 1986; Hastie and Tibshirani 1986). AVAS finds relationships by using smoothers to estimate condition expectations, and the parameters for these smoothers are chosen using generalized cross-validation which at least asymptotically should reflect prediction error (Friedman and Stuetzle 1982; Breiman and Friedman 1985; Hastie and Tibshirani 1986). Also, as we discuss below, the models tend to fit the series by measures other than r-square, particularly in anticipating turning points in the series.

The estimated transformations (Fig. 4) are similar for each of the six models for all variables. (AVAS calculates empirical transformations so the form of the transformation is determined by plotting the transformed variable against the original variable. All transformations are standardized to have zero mean and variance of 1; this is necessary for identification of the transformations.) Recruitment at time t is transformed to a form very close to a log transformation. This agrees with our observation of the decomposed recruitment series that the series appears to have increased variance at higher levels; the log transformation stabilizes the variance in this instance. A log transformation also means that environmental effects are on a proportional rather than an absolute basis, which, *a priori*, appears to be more sensible.

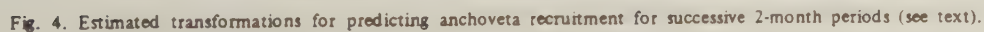
The estimated transformation for recruitment at time $t-2$ suggests two separate regimes - periods of relatively lower recruitment and periods of higher recruitment. The transformations suggest that the behavior is almost like an indicator function - the group, rather than the exact level, being the important information. At first glance, a 2-year lag in recruitment would seem to reflect the effect recruitment has on the spawning biomass for the recruits at the present time period. However, as previously mentioned, parent biomass during the spawning period is not a good predictor and adds little to our model. The mechanistic interpretation of the 2-year lag in recruitment therefore is an open question.

The transformation of transport during the previous September generally increases to a peak at around a value of 2.5, which corresponds to a wind speed of roughly 6 m/sec, decreases to a minimum with a value of 3, roughly corresponding to a wind speed of 7 m/sec and then increases again. Note that wind speeds between 6 and 7 m/sec correspond to the transitional level at which water changes from being hydrodynamically "smooth" to being hydrodynamically "rough" (Deacon and Webb 1962).

The transformation of transport in November generally increases, but behaves differently between the same values of 2.5-3. The model appears to be contrasting the September and November conditions. Optimal conditions occur when there is some transport in September followed by a high level of offshore transport in November. Again, the mechanistic interpretation of these variables is not clear.

The model for December-January recruitment also contains a term for September transport three months earlier, corresponding to the spawning period. The estimated transformation decreases monotonically, with a particularly sharper slope as wind speed exceeds the 6-7 m/sec range. This term appears to explain why the large egg production during the August through October period does not produce a large number of recruits: egg and larval mortality may be much higher. It is interesting that this is the only period during where conditions during spawning are important to the model.

On the whole, the model predictions (Figs. 5, 6 and 7) of transformed recruitment appear to be quite satisfactory. As the estimated transformations are close to being log transformations, the values are similar to taking the log of recruitment and then standardizing the variables. This will not change relative peaks and troughs and trends in the data. As is clear from both the fits and the residuals, none of the models do a very good job for the first five years, 1955-1959. After that, the models appear to track the major turning points quite well, in particular by anticipating the major decline in recruitment during the 1969-1971 period and the subsequent increase in recruitment later on in the 1970s. Apart from the first five years, the residuals are fairly well behaved except for the April-May residuals which show a definite trend throughout the model



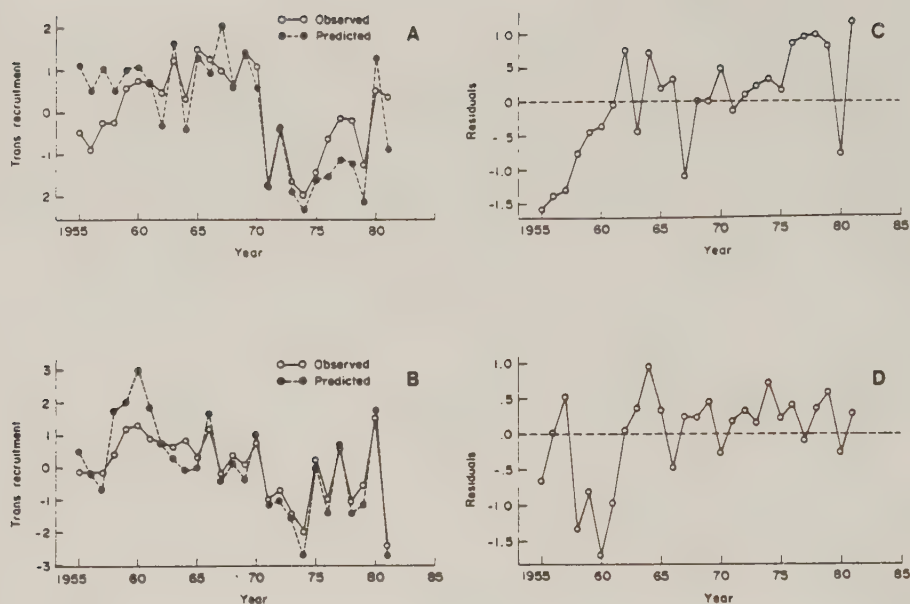


Fig. 5. Observed and predicted February-March (A) and April-May (B) anchoveta recruitments, with residuals (C, D).

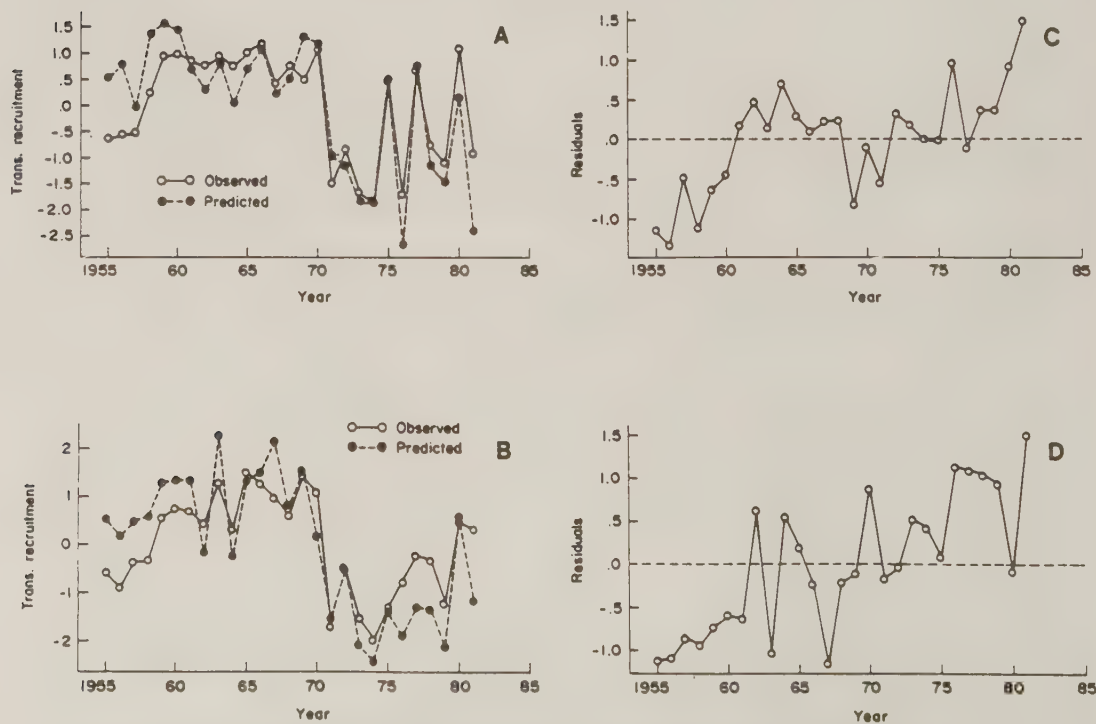


Fig. 6. Observed and predicted June-July (A) and August-September (B) anchoveta recruitments, with residuals (C, D).

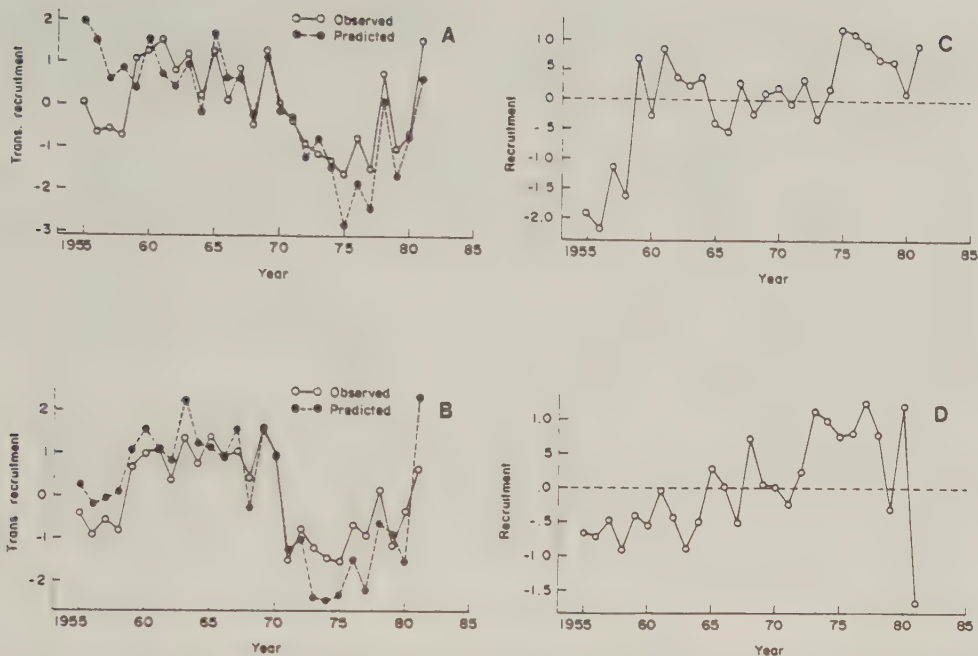


Fig. 7. Observed and predicted October-November (A) and December-January (B) anchoveta recruitments, with residuals (C, D).

period. The June-July and August-September models, when recruitment appears to be at or near a maximum, appear to anticipate changes in recruitment quite well.

The biomasses and the recruitment estimates for the period 1953 to 1959 were obtained through VPA using values of residual natural mortality (M_0) which could not be calibrated against independent biomass estimates; moreover, during this period, a large proportion of the withdrawals used for the VPA were estimates of anchoveta consumption by birds and bonito (see Pauly, Palomares and Gayanilo, this vol.). These appear to be sufficient reasons for differences between this period and the succeeding ones and thus explain why, in terms of our models, recruitment during this time period behaved in a manner different from the rest of the model period (see also Pauly, this vol.).

Discussion and Conclusions

We have shown that while the high degree of autocorrelation in the monthly recruitment data makes it difficult to identify causal models of anchoveta recruitment, we could, however, identify yearly models for bimonthly recruitment series. These models tend to have a similar structure, predict recruitment with approximately equal success and appear promising as a means to forecast future trends in anchoveta recruitment.

The pattern of the cross and partial correlation matrices, as well as several different modelling approaches, have all suggested the same basic models. Thus we feel confident that the relationships described in our models reflect the basic structure of the data. However, there is no clear biological interpretation of this structure. As we have done an extensive amount of searching through different sets of variables and estimating transformations to increase model fit, it is likely that our estimates of the goodness of fit of our models and of the ability of the models to predict future data is somewhat inflated. We would therefore recommend to implement the following steps before attempting to implement a model similar to the one analyzed here:

(i) Attempt to calibrate the estimated recruitment series with independent data (i.e., data not used in obtaining the estimates) to further verify that the estimated recruitment reflects the actual changes in recruitment, at least on a yearly basis;

(ii) Calculate offshore transport and wind speed cubed from other stations near Trujillo to check on the accuracy and consistency of this data set;

(iii) Develop a better mechanistic understanding of the underlying models. We are distrustful of forecasting models that do not have a clear biological interpretation and for which there is no independent evidence for the relationships developed in the exploratory analysis;

(iv) For log recruitment, use techniques that estimate transformations without transforming the dependent variable, and that allow for greater testing of model parameters, such as GAIM (Hastie and Tibshirani 1986); and finally

(v) Use generalized cross-validation or related techniques to test the stability of both the transformations and the degree of fit of the models, in order to get a better idea of the predictive capability of the models for data to be obtained in the future.

Despite these reservations, we feel we have shown that the series of recruitment estimates produced by Pauly, Palomares and Gayanilo (this vol.) have properties which enable them to forecast far enough in advance for consideration in the formulation of management actions. Further, we have indicated the importance of including variables that reflect environmental processes. However, the fact that the resulting models do not appear to conform to any of the conventional hypotheses concerning major influences on recruitment success remains unsettling.

Acknowledgements

This research was made possible through a cooperative agreement between the IMARPE-PROCOPA-ICLARM Project and the Pacific Fisheries Environmental Group, Southwest Fisheries Center. In particular we thank Dr. H. Salzwedel, PROCOPA Project Leader and Dr. Schmidt of GTZ for their support of the second author's stay in Monterey. We thank Dr. R. Villanueva, Executive Director of IMARPE, and Dr. Izadore Barrett, Director, Southwest Fisheries Center for allowing this cooperative effort. We also thank Dr. Daniel Pauly of ICLARM, Drs. A. Bakun and R. Parrish and our colleagues at IMARPE and PFEG for comments and support during the completion of this work. Prof. R. Tibshirani kindly provided us with a copy of the AVAS program and answered many questions about its use.

References

- Akaike, H., G. Kitagawa, E. Arahata and F. Tada. 1979. TIMSAC-78, Computer Science Monographs. The Institute of Statistical Mathematics, Tokyo. 11. 279 p.
- Bailey, K. M. 1981. Larval transport and recruitment of Pacific hake *Merluccius productus*. Mar. Ecol. Prog. Ser. 6:1-9.
- Bakun, A. 1973. Coastal upwelling indices, west coast of North America, 1946-71. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-671. 103 p.
- Bakun, A. 1986. Comparative studies and the recruitment problem: searching for generalizations. CalCOFI Rep. 26:30-40.
- Bakun, A. and R.H. Parrish. 1980. Environmental inputs to fishery population models for eastern boundary current regions, p. 67-104. In G.D. Sharp (ed.) Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, Peru, April-May 1980. IOC Workshop Rep. 28. Unesco, Paris.
- Breiman, L. and J.H. Friedman. 1985. Estimating optimal transformations for multiple regression and correlation. J. Amer. Stat. Assoc. 80:580-619.
- Cleveland, W.S. 1979. Robust locally weighted regression and smoothing scatterplots. J. Amer. Stat. Assoc. 74:829-836.
- Collins, R.A. and A.D. MacCall. 1977. The California Pacific bonito resource, its status and management. Calif. Dept. Fish and Game, Mar. Res. Tech. Rep. 35. 39 p.
- Deacon, E.L. and E.K. Webb. 1962. Small-scale interactions, Chapter 3. In M.N. Hill (ed.) The sea: ideas and observations on progress in the study of the seas. Interscience, New York.
- Efron, B. 1982. Transformation theory: How normal is a family of distributions? Ann. Stat. 10:323-339.
- Efron, B. 1986. How biased is the apparent error rate of a prediction rule? J. Amer. Stat. Assoc. 81:461-471.
- Friedman, J.H. and W. Stuetzle. 1982. Smoothing of scatterplots. Tech. Rept. Orion 3, Dept. of Statistics, Stanford University.
- Gersch, W. and G. Kitigawa. 1983. The prediction of time series with trends and seasonalities. J. Bus. Econ. Stat. 3:253-264.
- Hastie, T. and R. Tibshirani. 1986. Generalized additive models. Statistical Science 1:297-318.
- Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173:212-230.

- Lasker, R. 1981. Factors contributing to variable recruitment of the northern anchovy (*Engraulis ringens*) in the California Current: contrasting years, 1975 through 1978. In R. Lasker and K. Sherman (eds.) The early life history of fish: recent studies. The second ICES Symposium, Woods Hole, Mass., April 1979. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 178:375-378.
- MacCall, A.D. 1980. The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as *Engraulis*, p. 201-220. In G. Sharp (ed.) Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, Peru, April-May 1980. IOC Workshop Rep. 28. Unesco, Paris.
- Mendelsohn, R. and P. Cury. 1987. Fluctuations of a fortnightly abundance index of the Ivorian coastal pelagic species and associated environmental conditions. Can. J. Fish. Aquat. Sci. 44:408-421.
- Mendiola, B.R. and N. Ochoa. 1980. Phytoplankton and spawning of anchoveta, p. 242-253. In G.D. Sharp (ed.) Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, Peru, April-May 1980. IOC Workshop Rep. 28. Unesco, Paris.
- Mendo, J., L. Pizarro and R. Huaytalla. 1987. Reporte de datos sobre indices de afloramiento y turbulencia diarias para Trujillo y Callao, Peru, 1953-1985. Bol. Inst. Mar Perú-Callao 11:40-117.
- Parrish, R.H., A. Bakun, D.M. Husby and C.S. Nelson. 1984. Comparative climatology of selected environmental process in relation to eastern boundary current pelagic fish reproduction, p. 731-777. In G.D. Sharp and J. Csirke (eds.) Proceedings of the Expert Consultation to Examine Changes in Abundance and Species of Neritic Fish Resources, San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep. 291 (Vol. 3).
- Peterman, R.M. and M.J. Bradford. 1987. Wind speed and mortality rate of a marine fish, the northern anchovy (*Engraulis mordax*). Science (Wash.) 235:354-356.
- Santander, H. 1980. Fluctuations in spawning of anchoveta and some related factors, p. 255-274. In G.D. Sharp (ed.) Workshop on the Effects of Environmental Variations on the Survival of Larval Pelagic Fishes, Lima, Peru, April-May 1980. IOC Workshop Rep. 28. Unesco, Paris.
- Santander, H. and R. Flores. 1983. Los desoves y distribución larval de cuatro especies pelágicas y sus relaciones con las variaciones del ambiente marino frente al Perú. In G. D. Sharp and J. Csirke (eds.) Report of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, 18-29 April 1983. FAO Fish. Rep. 291(1):41-54.
- Santander, H. and S. de Castillo. 1973. Estudio sobre las primeras etapas de vida de la anchoveta. Informe. Inst. Mar Perú-Callao 41:1-30.
- Tiao, G.C. AND G.E.P. Box. 1982. Modeling multiple time series with applications. J. Amer. Stat. Assoc. 76:802-816.
- Tibshirani, R. 1987. Estimating transformations for regression via additivity and variance stabilization. J. Amer. Stat. Assoc. (In press)
- Tsukayama, I. and M. Alvarez. 1980. Fluctuaciones en el stock de anchovetas desovantes durante las temporadas reproductoras de primavera 1964-1978, p. 23-240. In G.D. Sharp (ed.) Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, Peru, April-May 1980. IOC Workshop Rep. 28. Unesco, Paris.
- Velleman, P.F. and D.C. Hoaglin. 1981. Applications, basics, and computing of exploratory data analysis. Duxbury Press, Boston. 354 p.

Fluctuations of a Fortnightly Abundance Index of the Ivoirian Coastal Pelagic Species and Associated Environmental Conditions

Roy Mendelssohn

Pacific Environmental Group, Southwest Fisheries Center, National Marine Fisheries Service, P.O. Box 831, Monterey, CA 93942, USA

and Philippe Cury

CRODT, B.P. 2241, Dakar, Senegal

Mendelssohn, R., and P. Cury. 1987. Fluctuations of a fortnightly abundance index of the Ivoirian coastal pelagic species and associated environmental conditions. *Can. J. Fish. Aquat. Sci.* 44: 408–421.

In this paper we analyze time series of catch per unit of effort (CPUE) from 1966 to 1982 of small pelagic species off the Ivory Coast using sea surface temperature (SST) collected by merchant ships. A fill-in model is used to estimate missing values of CPUE and SST in the areas in which the fishery operates. A multivariate time series model of the fortnightly data is able to explain 43% of the observed variance in CPUE from 1966 to 1982. A model estimated by using only the data from 1966 to 1980 produced reasonable forecasts of the fortnightly CPUE for 1981–82. A new approach for estimating optimal transformations of variables in the model is used to examine the form of the relationships between CPUE and its predictors. The biological interpretation of the estimated transformations is consistent with previous results on the dynamics of zooplankton in the same area.

Les auteurs analysent une série chronologique de prises par unité d'effort (PUE) de petites espèces pélagiques capturées de 1966 à 1982 au large de la Côte d'Ivoire en fonction des températures de l'eau en surface (TES) relevées par des navires marchands. Ils ont utilisé un modèle à blancs pour déterminer les valeurs manquantes des PUE et des TES pour les pêcheries exploitées. Un modèle des séries chronologiques à plusieurs variables aléatoires pour des données bimensuelles permet d'expliquer 43 % de la variance observée des PUE obtenues de 1966 à 1982. À l'aide d'un modèle généré par les données recueillies de 1966 à 1980, ils ont obtenu des prévisions acceptables des PUE bimensuelles pour 1981–82. Une nouvelle approche pour l'estimation des transformations optimales des variables du modèle est utilisée pour étudier la relation entre les PUE et leurs éléments extrapolés. L'interprétation biologique des transformations estimées est en accord avec les résultats antérieurs sur la dynamique du zooplancton dans la même région.

Received September 13, 1985

Accepted September 30, 1986
(J8413)

Reçu le 13 septembre 1985

Accepté le 30 septembre 1986

The purse-seine fishery for coastal pelagic species off the Ivory Coast annually lands around 20 000 metric tons; this makes the fishery of local socioeconomic importance. The fishery also is of scientific interest because coastal pelagic species are important worldwide and are believed to be significantly influenced by environmental factors (see for example Parrish et al. 1983). The fishery off the Ivory Coast occurs in a region with two upwelling seasons, a smaller one around January and a larger one later in the year, which are followed by periods of strong rainfall, which affects salinity levels in the environment of the fish. Understanding the fishery dynamics in this area and how the dynamics are influenced by the environment can increase our understanding of other pelagic fisheries of greater economic importance.

In this paper our primary goal is to model the relative impact of the environment on the availability of pelagic species off the Ivory Coast in Africa and the manner in which the environment affects the dynamics of catch per unit of effort (CPUE) for these species on time scales as short as 2 wk. Previous studies

suggest that the availability and abundance of these stocks are strongly influenced by the environment. Marchal (1967) and FAO (1974) presented evidence that sea surface temperature (SST) and salinity are important influences on the intrayear fluctuations in abundance of these stocks. Annual fluctuations in the abundance indices for the main Ivoirian or Ivoirian-Ghanaian stocks also have been related to changes in upwelling and rainfall (ORSTOM 1976; Binet 1982; Cury and Roy 1985). However, short-term fluctuations of these stocks never have been considered before.

Our approach to this problem is to use multivariate autoregressive moving-average (ARMA) models as described in Tiao and Box (1981) to model and forecast an index of relative abundance for the pelagic species off the Ivory Coast. We also use a new technique developed by Breiman and Friedman (1985) to analyze more closely the form of the relationship between CPUE and the relevant environmental variables. This technique allows us to examine the nonlinearities and discontinuities in the data that a priori are believed to exist but whose

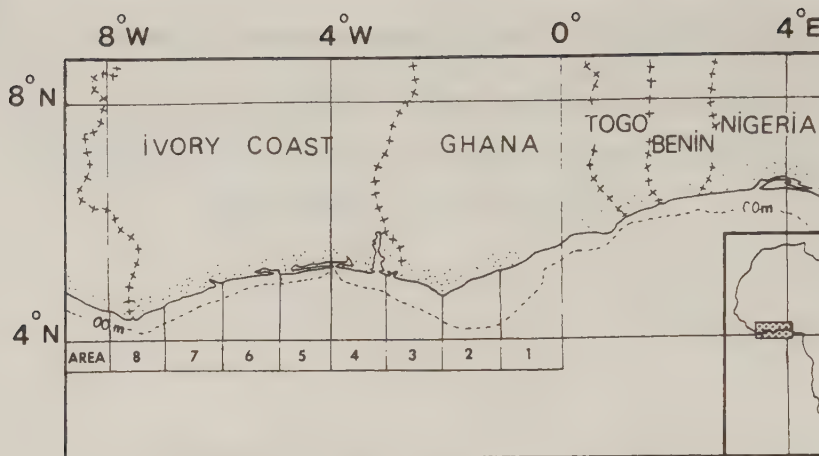


FIG. 1. Location of the areas studied off the Ivory Coast.

exact forms are not known. This should increase our theoretical understanding of how the environment affects the fish stocks as well as have important implications for modeling of fish abundance.

The ARMA class of models are stochastic rather than deterministic and have been of increasing interest in both applied and theoretical aspects of economics and engineering (among other areas). They emphasize the variation in the data and use empirically based methods to determine the proper form of the model. There have only been a few attempted applications of these techniques to fisheries problems (Boudreault et al. 1977; Saila et al. 1980; Mendelsohn 1981).

In contrast with our stochastic models, the majority of fishery management models developed over the last decades have been deterministic models concerned with estimating characteristics of the population at equilibrium (see for example Schaefer 1954; Beverton and Holt 1957; Ricker 1958; Pella and Tomlinson 1969; Fox 1970). Typically, these deterministic models operate on a yearly time scale, and in the best cases provide information related to optimal management of a fishery (such as maximum sustained yield (MSY)) and information necessary to determine policies to achieve this maximum, such as yield per recruit, age of first capture, and other characteristics of the exploited stocks.

Stochastic models of fisheries can be used for forecasting, even if only for short-term forecasts such as a fortnight or a month ahead, and remedy some of the deficiencies of deterministic models. They can be used to improve planning by fishermen and buyers, including both artisanal processors and industrial firms. Many of the exogenous changes that affect a fishery, such as price, or more to the point of this paper, the fluctuations in the physical environment, occur at time scales much shorter than a year. Such stochastic models can improve fishery management by defining the expected level of variation in a fishery and how much of the variation is due to environmental influences.

Biological Data

The fishery exploiting the pelagic species off the Ivory Coast consists mainly of purse seiners that are based in Abidjan. The fishery began in 1955 and expanded rapidly after that. De-

pendable statistics for the fishery have been available only since 1966 (FAO 1974). The fishery operates mainly over the rather wide continental shelf that exists off the Ivory Coast and Ghana. We have divided the area off the Ivory Coast and Ghana into eight zones, each 1° of longitude and extending from latitude 4°N to the coastline (Fig. 1). Areas 4-7 are the major fishing zones; catch in area 8 is typically less than 1% of the total annual catch, and the areas 1-3 off the coast of Ghana have only been exploited by the Ivoirian purse seiners at irregular intervals. The catch in these areas is dominated by *Sardinella aurita*, which is not the dominant species in the Ivoirian fishery.

During the period 1966-82, *Sardinella maderensis* was the dominant species caught in areas 4-7, comprising 54% of the total catch (Table 1; Fig. 2). *Brachydeuterus auritus* comprised 16.5% of the total catch during the same period, and various other species (Engraulidae, Scombridae, and Carangidae) comprised 14.6% of the catch. All of these species appear to be mainly Ivoirian stocks, as the catch of these species off the coast of Ghana appears to be coming from different stocks (FAO 1974). *Sardinella aurita*, which comprised 12% of the total catch, and *Scomber japonicus*, which comprised 2.4% of the total catch, appear to be shared stocks that are found off the coast of both countries (FAO 1974). *Sardinella aurita* and *S. japonicus* essentially disappeared from the catches in 1973, probably due to a combination of overfishing the previous year and due to anomalous climatic events in 1973. Binet (1982) has discussed this for *S. aurita*. The reasons for the disappearance of *S. japonicus* has not been conclusively determined. *Sardinella aurita* reappeared in 1976 and its relative abundance increased sharply off the Ivory Coast during 1981 and 1982.

The raw data consist of daily records for each boat and for each trip including the areas fished, the areas visited, and the catch. Search time was calculated for each area and fortnight using the method described in Fonteneau and Marchal (1970) and was used as a measure of fishing effort. CPUE was calculated by dividing the total catch of all species in an area during a fortnight by the corresponding search time for that area. When there was no fishing effort the CPUE was assumed to be a missing data point, as the lack of fishing does not necessarily imply the lack of fish. CPUE for the entire area was calculated as the mean of the CPUE for the four zones. CPUE thus is

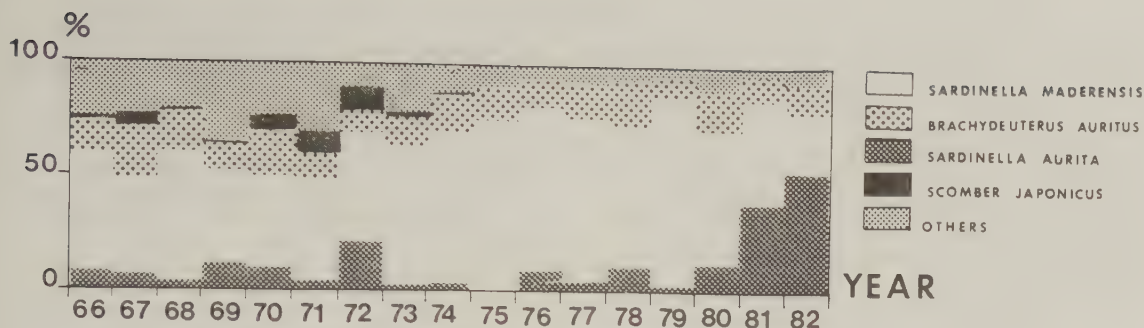


FIG. 2. Specific composition of the total catch of the Ivorian purse seiners in the main fishing areas (zones 4-7).

TABLE 1. Total catch (metric tons) per species for areas 4-7 from 1966 to 1982.

	<i>S. maderensis</i>	<i>B. auritus</i>	<i>S. aurita</i>	<i>S. japonicus</i>	Others	Total
1966	9 305	3662	1 783	262	4697	19 708
1967	8 944	6678	1 886	1405	5389	24 302
1968	12 150	5170	1 165	296	4611	23 391
1969	6 288	2745	2 301	100	5838	17 271
1970	5 794	3477	1 726	1195	3553	15 746
1971	8 629	2718	1 112	2131	5870	20 459
1972	10 742	3000	5 553	2485	2029	23 808
1973	5 368	1275	179	217	1775	8 815
1974	6 823	1850	268	61	1261	10 263
1975	7 805	1639	10	0	956	10 410
1976	10 974	2000	1 457	11	866	15 310
1977	14 898	3413	855	0	1398	20 563
1978	10 325	3568	1 892	6	923	16 716
1979	14 709	1208	439	0	912	17 268
1980	8 196	2572	1 789	0	1616	14 171
1981	9 790	2418	8 747	4	836	21 796
1982	5 108	2463	10 637	0	1608	19 815

defined in units of metric tons per day of fishing.

For CPUE to reflect the abundance of a fish that schools and whose schooling behavior changes rapidly, the measure used should reflect the number of schools present and the size and spatial distributions of both the fleet and the stock. Ignoring fishing, the boats can be viewed as taking a sample during each time period to provide an estimate of the abundance of the fish stock. From sampling theory we know that if there are too few boats out "sampling" (fishing) or if their spatial distribution is not appropriate to the target population, the estimates of abundance will be very inaccurate. Similarly, sampling needs to reflect the relative frequency of different school sizes if abundance estimates are to be accurate.

The measure of effort we use considers total search time, but does not consider either the number of boats searching or school size distribution. Thus, our measure will not always reflect abundance, particularly when there have been only a few boats out searching. More boats searching should also produce a less variable estimate of CPUE due to a more uniform coverage of the fishing area. This may explain the increased variability in the CPUE series after 1973, when the number of boats fishing decreased from 40 to fewer than 20.

Environmental Data

The environmental series considered in preliminary model identification consist of SST data collected by merchant ships

passing through the area. The SST data were obtained from the National Climate Center (U.S.), and values were checked against a long-term atlas and further verified by C. Roy of ORSTOM. Fortnightly mean values then were calculated for the SST series by area, to agree with the fishery data, and for the two coastal environmental series.

The continental shelf off the Ivory Coast is influenced by two periods of upwelling. The main upwelling season occurs from June to September and a second, smaller upwelling occurs in January and February (Morliere 1970). The physical mechanisms underlying these upwellings are summarized and discussed in Picaut (1983, 1985). One of the reasons SST was selected as an environmental series is that it should be a reasonable surrogate variable for the occurrence of upwelling in the region.

Preliminary Data Analysis

Preliminary analysis of the data is necessary for two reasons. We consider areas that have no fishing as having missing data points and there are also areas with missing environmental data; most of our techniques, however, require complete data series. Therefore we must fill in the missing data in a manner that will not distort the underlying relationships in the data.

Also, the ARMA approach to model building is empirical, using properties of the covariance structure of the data to determine the appropriate form of the model to be estimated, rather

than hypothesizing a model a priori. The form of the estimated lagged covariance matrices and generalized partial-correlation matrices are used to make initial estimates of the appropriate lags and variables to be included in the model.

The first step in the preliminary analysis is to fill in the missing data by area. Areas 4–7 have roughly 4% of the CPUE data missing. Also, during the years 1969 and 1982 there was a large gap in the SST data in all the areas. The CPUE data were filled in using an algorithm by Shumway and Stoffer (1982), used successfully in a related analysis by Mendelsohn and Roy (1986). The algorithm is described in the Appendix.

The basic idea of the algorithm is to iteratively fit a lagged model to the completed series and then to calculate minimum mean-square estimates of the missing data given the new parameter estimates. The algorithm has good statistical properties (see Shumway and Stoffer 1982), particularly in terms of preserving the covariance structure of the observed series. Other more obvious methods do not share this property. Also, the algorithm includes observation error in calculating both the parameter estimates and the smoothed estimates of the missing data.

The algorithm calculates smoothed values rather than predicted values of the missing data. Predicted values use only information previous (or perhaps contemporaneous) to the missing data point to estimate the fill-in. Smoothed values use all the information available consistent with the model. Thus, for an AR(2) model, the filled in value is calculated from a forward model using data from the last two periods, from a backward data using the next two periods of data, and from a regression-like model using contemporaneous innovation series.

The fill-in model for CPUE uses the observed data from each area and the model form to fill in any missing point. While this may cause some bias in our later analysis, it is a conservative procedure for several reasons. First, as one of our main interests is the role of the environment in the population dynamics, any bias introduced should be to lessen the importance of the environment as a predictor and to increase the importance of lagged values of CPUE as predictors. Also, we use average CPUE (across areas) in our final model. Thus most of the filled in values are averaged with real values from other areas, lessening the impact on the data of any of the filled in values. With only 4% of the data missing, a filled in data point would have to have significant leverage to greatly influence the final model.

The SST data were filled in using both the Shumway and Stoffer algorithm and the estimated seasonal cycle. The iterative algorithm produced data values for the missing blocks in 1969 and 1982 that did not appear reasonable; however, the spectra produced by this procedure were very consistent with those calculated from complete subseries of the SST data. Parameter estimates depend on the covariances of the data, so that the bad data values may not be important. Using the estimated seasonal cycle can produce its own distortions, as the missing year may have been very unlike the normal year. This can greatly emphasize the seasonal frequency in the data while lessening other frequencies that might be of importance in determining the appropriate model.

Fortunately, our results were almost identical for each method of filling in the SST data. Preliminary reviewers of our results felt more comfortable with using the estimated seasonal cycle; therefore, in what follows, the SST data have been completed using the estimated seasonal cycle.

The smoothed values for CPUE by area (Fig. 3) appear to be quite reasonable. None of the estimated values appear as particular outliers, which reinforces our belief that this should produce little bias in our final calculations.

We do not use effort at time t (i.e. no lag) as a predictor because this would introduce a large bias and a high degree of spurious correlation into the analysis. This point is shown mathematically in Eberhardt (1970); Mendelsohn (1981) gives other references that examine the degree of spurious correlation introduced.

An intuitive explanation of the source of this spurious correlation can be seen by considering $\log(\text{CPUE})$ which equals $\log(\text{catch}) - \log(\text{effort})$. If this is regressed against a function of effort, then effort is clearly on both sides of the equation. If the coefficient of variation (CV) of catch is small compared with that of effort, then catch can be viewed as a constant, and we would be regressing a function of effort (the logarithm of effort) against another function of effort, so that some degree of fit is assured. Simulations in the references suggest that the r^2 value can be inflated by as much as 0.4–0.6 depending on the relative values of the CV of catch compared with the CV of effort.

The accuracy of the completed time series of CPUE and SST (Fig. 3 and 4) can be assessed in several ways: by comparing smoothed values with observed values when both exist; and by comparing smoothed values with observed values in other series where the data exist to check that the smoothed value is consistent. For the CPUE series, which are relatively complete, the smoothed values can be seen to be very close to the observed values, even at large peaks in CPUE, such as in area 4 during 1976 (Fig. 3a).

The parameter estimates produced by the AR(2) fill-in model for CPUE (Table 2) are of interest by themselves, as they appear to agree with and clarify previous work on migration in the stocks. The interpretation of the model for CPUE will be discussed in detail in a companion paper on the spatiotemporal dynamics of the fish. In what follows, we restrict our attention to CPUE and SST averaged over all of the areas.

Model Identification and Estimation

We model the temporal dynamics of CPUE and its possible relationships with SST by using for the most part the ARMA approach described in Tiao and Box (1981) and implemented in the computer program WMTS-1 (Tiao et al. 1980). At times, a method due to Akaike et al. (1979) for subset multivariate autoregression identification was also used to help select the appropriate lags and the parameters to be included in the model at those lags.

For several reasons, we analyze the natural logarithm of CPUE (actually of $\text{CPUE} + 0.05$ so that zero values are well defined) rather than analysing CPUE itself. First, CPUE is a ratio of two separate series, and ratios rarely are linear or gaussian in distribution. Taking logarithms of the data produces a new series that is the difference of the logarithms of the two original series, which should have better statistical properties. Second, inspection of the raw data (Fig. 4a) suggests that the variance of the series changes with the level of the CPUE series. A range–mean plot (Jenkins 1979, p. 96) of the CPUE data was calculated. This is found by dividing the series into a number of subseries (in this case years), calculating the range and mean of each subseries, and plotting the range versus the mean. This plot showed that a transformation such as a log

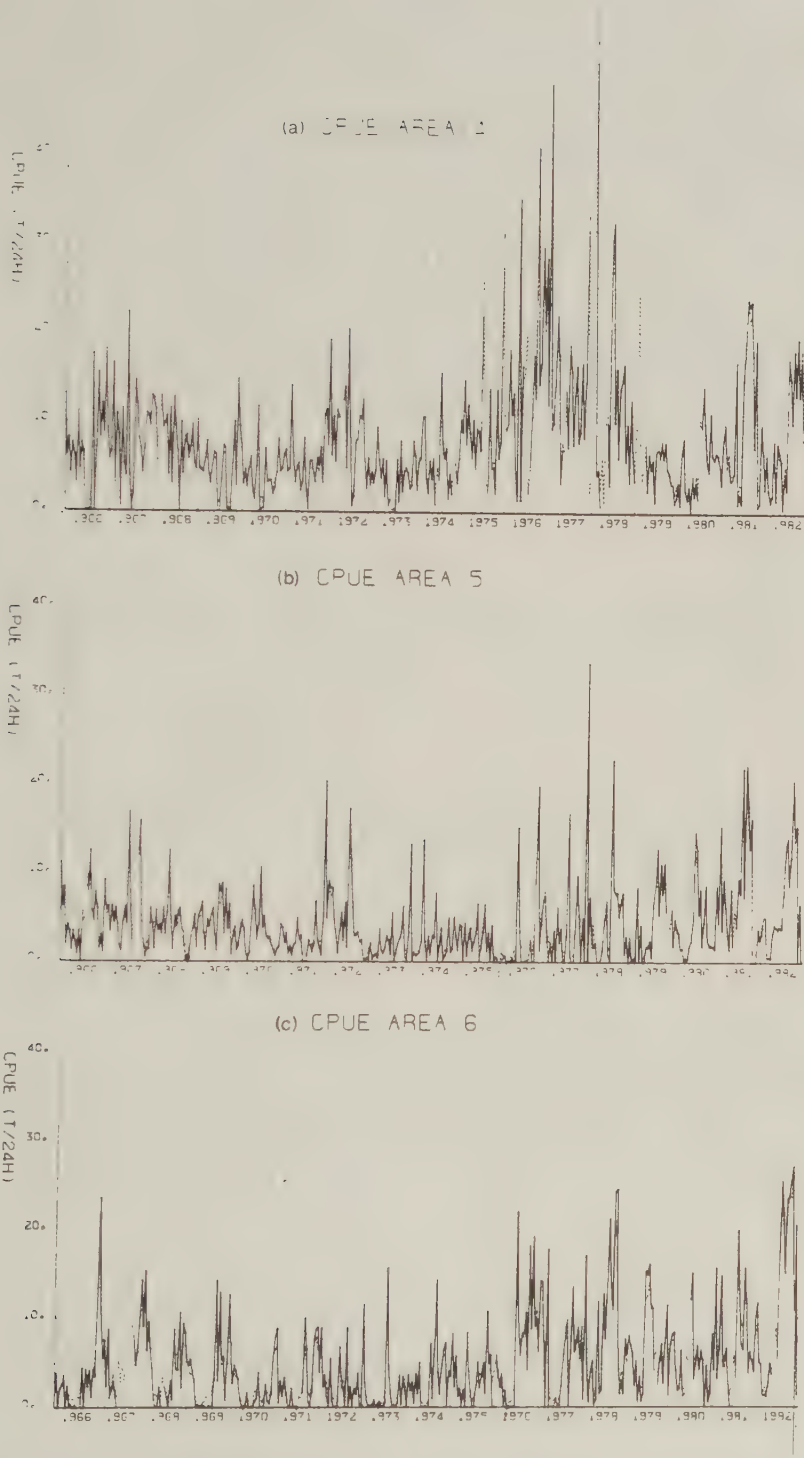


FIG. 3. Time series of CPUE (all species) for (a-d) areas 4-7 and (e) all areas combined. Solid lines = observed; broken lines = smoothed. (Fig. 3 concluded next page)

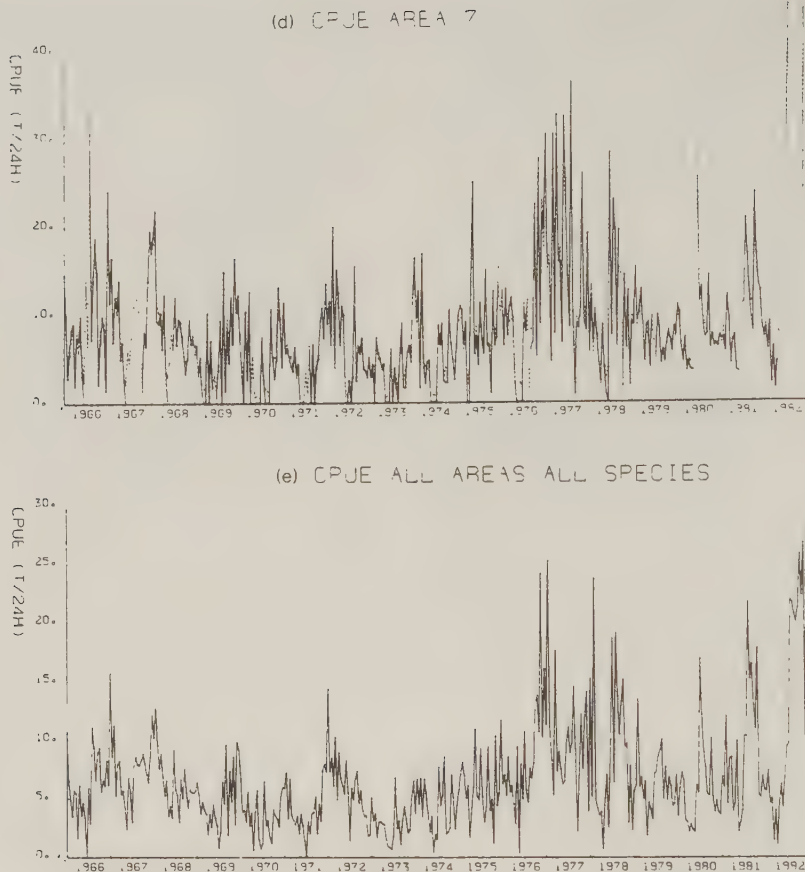


FIG. 3. (Concluded)

transform or a negative square root transformation was needed. Third, there are theoretical reasons for believing that a log scale is more appropriate for modeling the interaction of CPUE with SST. On the untransformed scale, a 1° change in SST would have to make the same absolute change in CPUE at very low levels of CPUE as with very high levels of CPUE. When $\ln(\text{CPUE} + 0.05)$ is used, a 1° change in SST produces a percentage change in the level of CPUE rather than an absolute change. Thus, at much smaller levels of CPUE, smaller absolute changes in the level will be observed. In the next section, we will examine in more detail the proper scales for each of the variables in our model and the form of the interactions between the different variables.

The first step of the analysis is to identify the appropriate lags to be included in the model and whether an AR, MA, or ARMA model is more appropriate. This is done by examining the cross-correlation matrices and by calculating the general partial-correlation matrices (see Tiao and Box 1981 for details). The CPUE autocorrelation function (not shown) has significant lags up to 8 fortnights, and again around 24 fortnights (1 yr), although the pattern is not that of a seasonal cycle in the data. (A seasonal cycle is reflected in a sinusoidal autocorrelation function. The autocorrelation function of SST is

sinusoidal, reflecting a seasonal cycle, while CPUE only has a peak at a lag of 24 fortnights. To call this a "cycle" would be equivalent to saying a peak at lag 1 shows a one-fortnight cycle.) The pattern in lags 1–8 suggests significant values at lags 1, 2, and 4 and possibly at lag 6. This is because autoregressive terms decay exponentially. Thus, if there is a significant autocorrelation at lag 1, then lag 2 will have an autocorrelation of that value squared, even if there is no lag 2 effect. Similarly, if there is a lag 2 term, then lag 4 will have that value squared even if there is no lag 4 effect. Thus, we look for the autocorrelations that stand out from the exponential decay of the previous significant lags.

The cross-correlation function (not shown) shows a significant peak and exponential decline with SST lagged 17 fortnights and significant cross-correlations with SST lagged until about 8–10 fortnights. The generalized partial-correlations (Table 3) exhibit "spiked" behavior consistent with an AR-type model at the lags suggested by the cross-correlation matrices.

An exact maximum likelihood algorithm was used to estimate the parameters of this model, which also included parameters modeling the SST series. This last step is important so that the final vector residual series are as close as possible to independent multivariate gaussian variables. Otherwise, the esti-

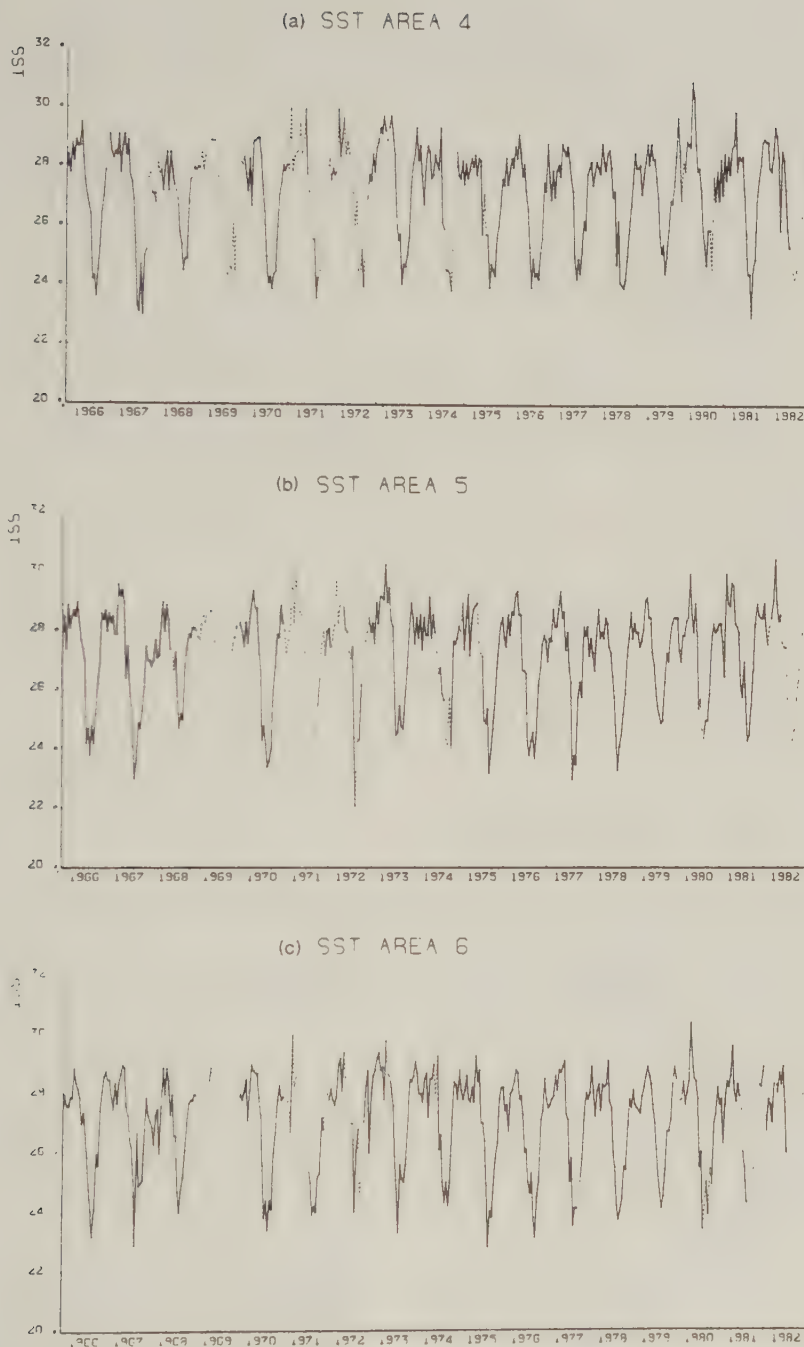


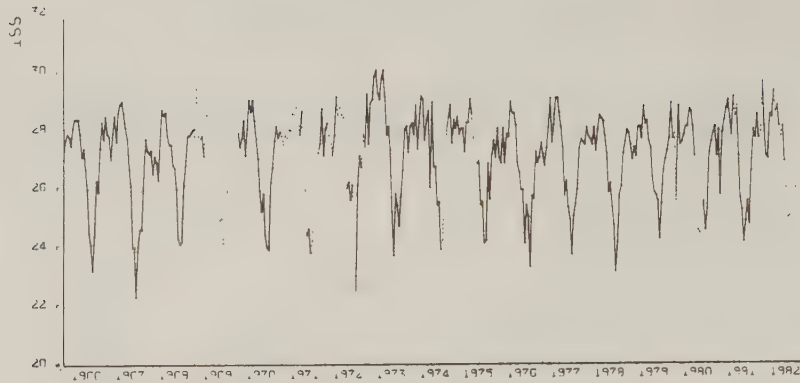
FIG. 4. Time series of SST for (a-d) areas 4-7 and (e) average of all areas. Solid lines = observed; broken lines = smoothed. (Fig. 4 concluded next page)

mates can be biased. The relationships between CPUE and SST at lags 6 and 7 were found to be nonsignificant. They were discarded from the model, and the remaining parameters were reestimated.

The final parameter estimates and their standard errors

(Table 4a) were tested for adequacy by several methods. The residual cross-correlation matrices do not suggest a lack of fit (Table 5). The residual series (not shown) have a zero mean and otherwise do not suggest a lack of fit to the data. The normalized residuals for CPUE (not shown) are nearly gaus-

(d) SST AREA 7



(e) SST ALL AREAS

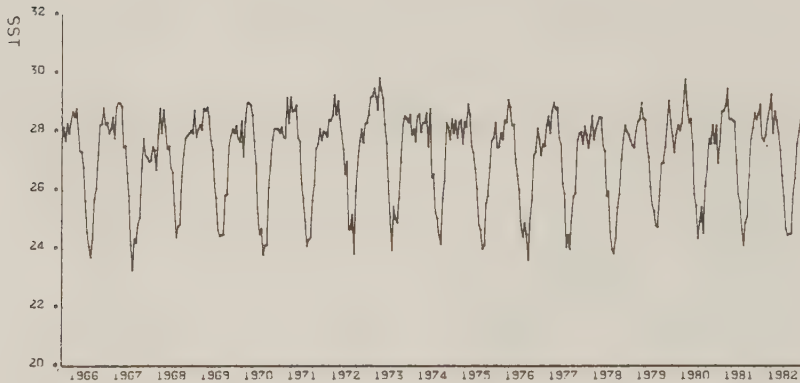


FIG. 4. (Concluded)

TABLE 2. Values of coefficients of the fill-in models for CPUE time series ($t-1$, $t-2$) in areas 4-7.

	Area 3		Area 4		Area 5		Area 6		Area 7		Area 8	
	$t-1$	$t-2$	$t-1$	$t-2$	$t-1$	$t-2$	$t-1$	$t-2$	$t-1$	$t-2$	$t-1$	$t-2$
Area 4	0.11	0.02	0.24	0.20	0.20	0.10	-0.51	0.34	0.22	0.06	0.11	-0.05
Area 5	0.01	-0.02	-0.07	0.19	0.40	0.09	0.02	0.07	-0.04	-0.14	-0.01	-0.11
Area 6	0.07	-0.03	0.08	-0.01	0.04	-0.01	-0.38	0.18	-0.02	0.10	0.17	-0.14
Area 7	-0.01	-0.16	0.08	0.09	0.09	-0.05	-0.04	0.44	0.31	0.53	-0.10	-0.13

TABLE 3. Significance (5%) of partial autoregression coefficients by lag for time series of CPUE and SST.

	Lag									
	24	17	1	2	3	4	5	6	7	8
LNCPUE	+		+	+		+				
SST	-	+	-	+				-	-	

sian, with a mean of zero and a median close to zero. The distribution of the normalized residuals is fairly symmetric also. There are two noticeable outliers, each with a normalized value greater than 4. These two points account for almost 10% of the residual variance. Both are from fortnights when there

was only one boat searching, and from the data it is quite clear that in each instance the boat was just passing through the area to fish in another area. This is consistent with our previous discussion of problems with the measure of effort used.

The model was also estimated using the fill-ins for SST produced by the Shumway and Stoffer algorithm (Table 4b). There is essentially no difference, giving us some confidence that our model is robust to the method of completing the data series. Both models were reestimated for the years 1966-82. In 1981 and 1982, there was a sharp increase in the level of CPUE, and also a change in the species composition, with an increasing amount of *S. aurita* in the catch. Even with these changes, there is essentially no change in the parameter values. Thus the estimated model appears to be robust to additional

years of data, even to data that are seemingly different from the previous years.

The estimated model for CPUE from the years 1966–80 is

$$\begin{aligned} \text{LNCPUE}(t) = & 0.248 \cdot \text{LNCPUE}(t-1) \\ & + 0.254 \cdot \text{LNCPUE}(t-2) \\ & + 0.162 \cdot \text{LNCPUE}(t-4) \\ & + 0.143 \cdot \text{LNCPUE}(t-24) \\ & - 0.143 \cdot \text{SST}(t-1) \\ & + 0.112 \cdot \text{SST}(t-2) \\ & + 0.044 \cdot \text{SST}(t-17) \end{aligned}$$

where $\text{LNCPUE}(t) = \ln(\text{CPUE}(t) + 0.05)$ and t references the time period in fortnights. The model explains 43% of the observed variance in the data. Without the two outliers, the model explains almost 55% of the observed variance. Observed and one-step-ahead predicted values of CPUE transformed back to the original scale (Fig. 5) show that the predicted values are close to the observed values except at the large peaks in CPUE. Also, the predicted values are generally better before 1973 than after, which may be due to the problems in effort mentioned earlier. The model also frequently predicts the beginning and end of the fishing season (see for example 1968, 1974, 1979, and 1981).

A scatterplot of the observed CPUE versus the predicted CPUE (not shown) shows a trend to underpredict at high levels of CPUE, particularly at values greater than 12 tons per day. In the next section we will discuss some reasons for this observation.

Interpretation of the Model and Examination of the Form of the Relationship between CPUE and its Predictors

An empirically derived model is more satisfying if it has an interesting biological interpretation which is consistent with or combines previous observations on the fishery. The model estimated in the last section has such an interpretation. All else being equal, CPUE will show some persistence on its own; at low levels it will tend to remain low and higher levels will exponentially decline at a reasonable rate. If a "kick" comes that pushes CPUE up to a higher level, then the results of this "kick" will be felt for a few time periods to come. This may be due to schooling behavior. Conditions favorable for the formation of large schools tend to persist so that the schools themselves are available to the fishery for an extended period.

From the model estimates, what appears to provide the needed "kick" is a drop in SST from two fortnights ago to one fortnight ago. The sharper the drop in temperature and the longer the duration of the drop, the greater the effect on CPUE. If SST was relatively warm two fortnights ago and relatively warm one fortnight ago, there will not be much change in CPUE. Similarly, if SST was relatively cold two fortnights ago and relatively cold one fortnight ago, again there will not be much change. Once the increase is started, it will be maintained for a while by the persistence of CPUE noted above. Thus, it is not colder or warmer waters per se that are conducive to high levels of CPUE, but rather a long and sharp drop in temperature. This is of course the behavior of SST at the onset of the upwelling seasons. The model suggests that the beginnings and endings of fishing seasons should be related to upwelling and the success of the fishing season related to whether the

TABLE 4. Final estimates and estimated standard error of the parameters from time series analysis from 1966 to 1982 and 1966 to 1980 using the (a) seasonal cycle and (b) iterative algorithm to fill-in SST series.

Parameter	1966–82		1966–80	
	Estimate	SE	Estimate	SE
<i>(a) Seasonal cycle</i>				
Lag 1 LNCPUE	+0.258	0.047	+0.224	0.051
SST	-0.143	0.039	-0.122	0.043
Lag 2 LNCPUE	+0.254	0.051	+0.223	0.054
SST	+0.112	0.038	+0.090	0.042
Lag 4 LNCPUE	+0.162	0.048	+0.171	0.051
SST	—	—	—	—
Lag 17 LNCPUE	—	—	—	—
SST	+0.029	0.013	+0.045	0.013
Lag 24 LNCPUE	+0.144	0.042	+0.131	0.044
SST	—	—	—	—
<i>(b) Iterative algorithm</i>				
Lag 1 LNCPUE	+0.261	0.047	+0.234	0.051
SST	-0.141	0.043	-0.117	0.046
Lag 2 LNCPUE	+0.257	0.051	+0.227	0.054
SST	+0.114	0.042	+0.089	0.045
Lag 4 LNCPUE	+0.159	0.048	+0.169	0.051
SST	—	—	—	—
Lag 17 LNCPUE	—	—	—	—
SST	+0.038	0.013	+0.042	0.014
Lag 24 LNCPUE	+0.148	0.042	+0.130	0.045
SST	—	—	—	—

season had strong or weak upwelling. Binet (1976) has presented results that show a correlation between a drop in SST and an increase in zooplankton biomass a fortnight later. Binet (1983) also has suggested that the colder waters tend to increase the aggregation of the zooplankton at the surface, and hence presumably to aggregate the fish as well. It is during the upwelling seasons with the onset of colder waters that we find higher levels of CPUE (Fig. 4e). As the fish species in our model feed on zooplankton (Dia 1972), this explanation of the physical mechanism underlying the model would appear to be consistent with independent biological observations.

E. Marchal (Antenne ORSTOM, Centre Oceanologique de Bretagne, Brest, pers. comm.) has suggested that CPUE lagged on itself at periods of 2, 4, 6, and 8 arises from the affect of the lunar cycle on these species noted in Marchal (1967). He also suggested that the residual correlation at lag 35 is approximately the correct lag at which the lunar and solar fortnights would be in phase. Thus, some of the long-term (four fortnights) persistence in CPUE may be due to this lunar effect.

So far we have restricted ourselves to linear models, with only a minor transformation in the CPUE data. There are a priori reasons to believe that the relationships between CPUE with itself lagged in time and between CPUE with SST at the various lags are nonlinear and that there may be possibly nonlinear transformations of the data that would improve the fit of the model while still maintaining an additive model which has better statistical properties. Plots of LNCPUE at time t versus SST at time t and $t-1$ (not shown) suggest a discontinuity or threshold in the relationship around approximately 27°C. These plots do not correct for the effect of the other variables in the model.

TABLE 5. Residual cross-correlations from lag 1 to 36 ("+" denotes a significant value and "-" a nonsignificant value at 5%).

Lag	CPUE	SST
1	-	-
2	-	-
3	-	-
4	-	-
5	-	-
6	-	-
7	-	-
8	-	-
9	-	-
10	-	-
11	-	-
12	-	-
13	-	-
14	+	-
15	-	-
16	-	-
17	-	-
18	-	-
19	-	-
20	-	-
21	-	-
22	-	-
23	-	-
24	-	-
25	-	-
26	-	-
27	-	-
28	-	-
29	-	+
30	-	-
31	-	-
32	-	-
33	-	-
34	-	-
35	+	-
36	-	-

To find "good" transformations of the data, we used a technique developed by Breiman and Friedman (1985) that empirically calculates optimal transformation of the data (see Appendix for further descriptions). The results of the algorithm are a smoothed empirical transformation of each of the observed data points. The implied functional form can be found by plotting the transformed value of the variable versus the original value. The transformed values are in no particular units (unless a functional transformation can be discerned from the plot; then the transformed data would be in whatever units are implied by that particular functional transformation).

In our model, the response variable is CPUE at time t , and the predictor variables are CPUE at times $t - 1$, $t - 2$, $t - 4$, and $t - 24$ and SST at times $t - 1$, $t - 2$, and $t - 17$. The resulting transformed model explains 59% of the observed variance in the original series. It is worth emphasizing that this is not necessarily the optimal transformed model. We used the lags and parameters identified in our linear model as the correct ones. It is possible that if the correct transformations had been known a priori, then other lags of either CPUE or SST would have been found to be more important as predictors of CPUE at time t . Also, slightly different results are obtained for CPUE depending on which set of fill-ins is used for SST.

The optimal transformations for CPUE and for CPUE lagged one fortnight (not shown) range between a linear to a log transformation; the most noticeable difference from a log transformation is that the curve is less flat at high values of CPUE (>12). The results suggest that a slightly less steep transformation might have been preferable.

The transformation for CPUE lagged four fortnights (Fig. 6a) shows a sharp discontinuity in the relationship. The transformation is almost piecewise linear with a point of discontinuity around 12 tons per 24 h of search. Beyond this point, the value increases sharply. It does not seem coincidental that this is the same value at which we find our model consistently underpredicting CPUE. Our best guess is that this result has to do with schooling behavior of the fish: first that such behavior may influence our measure of effort, and hence influence CPUE (discussed earlier in the paper), and second that once either large schools are formed or perhaps many schools are formed, the fish become much easier to find so that CPUE sharply increases. Why the sharpest discontinuity should be at a lag of four fortnights is not obvious, but is clearly a topic for further study.

We would expect that the relationship between CPUE and SST would be nonlinear, probably some type of threshold function. This is because there are temperatures too high for the *Sardinella*, so an increase in SST above some given temperature will not affect CPUE significantly, and similarly there is also probably a temperature too low for the species. The transformation for SST at a lag of one fortnight (Fig. 7a) decreases linearly to 28°C, increases to 28.5°C, and then again sharply decreases. Not surprisingly, the sharpest response is between 27 and 28°C. The reason for the change in sign at 28°C is unclear, but it is clear that the linear relationship of the original model will only roughly approximate this functional form. The transformation of SST at a lag of two fortnights (Fig. 7b) displays the expected threshold effect; it linearly increases to just short of 28°C and then levels off. Further increases in SST will not affect CPUE further. Marchal (1967) studied 1 yr of data and found 23–26°C to be the optimal temperature range and reported a sharp drop in CPUE between 28 and 29°C. Our transformation clearly supports this finding and shows that it is valid for more than the single year Marchal studied.

The transformation for SST lagged 17 fortnights (Fig. 7c) is not as easily interpreted. It is highly nonlinear, almost bimodal in form. E. Marchal (pers. comm.) has suggested that the relationship with SST 17 fortnights earlier possibly may be due to the effect on an earlier life stage of the fish.

The transformations show that our simple linear models will be adequate over some of the range of the observed data, but that there are sharp discontinuities that will cause systematic bias in the predictions. These results also show that we can find additive models with all the variables transformed to a proper scale that remove most of the difficulties. The nonlinear form of the transformations do not alter on the whole the physical interpretation of our model: indeed, except for the effect of CPUE lagged four fortnights, it would seem to reinforce it. The transformation of CPUE lagged four fortnights may reflect schooling behavior and changes in school size and distribution because of the sharp nonlinearity in the transformation for values greater than 12 tons per day of searching. More accurate forecasts could probably be developed using measures of CPUE that better reflect both the spatial and size distribution of the schools and the number of boats searching.

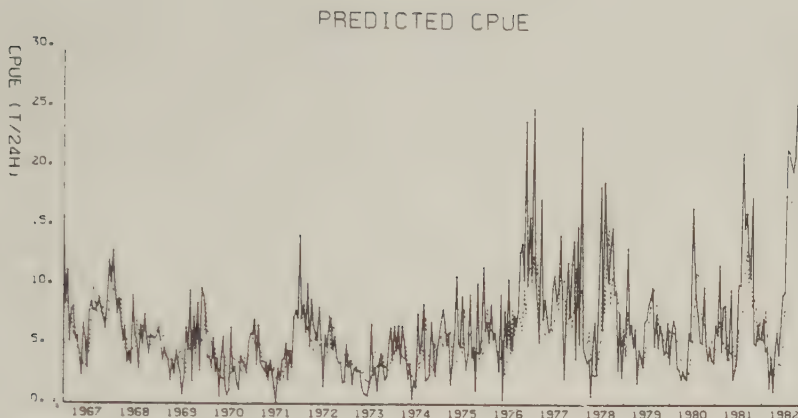


FIG. 5. Observed (solid line) versus predicted (broken line) CPUE from 1967 to 1982.

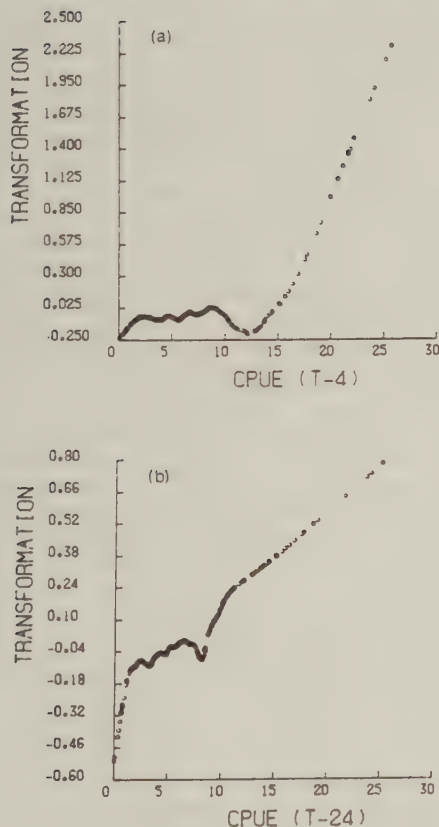


FIG. 6. Estimated optimal transformations of CPUE.

Forecasts

To test the ability of the model to forecast, the parameter values used were those estimated only from the data for the years 1966–80. The natural logarithm of CPUE was used in the forecasting model as discussed previously. The other transformations discussed in the previous section were not used in

calculating the forecasts. Making use of these transformations to improve the forecasts is an area of future research. The estimated model then was used to produce one-step-ahead forecasts for the years 1981 and 1982 with no further reestimation of the parameters. This is similar to what might have been done at the end of 1980 if real-time data had been available, that is, if at the end of each fortnight we had been able to obtain the CPUE and SST data for that fortnight in order to produce the next period's forecast. With the present data collection system, real-time data are not available. However, real-time data could be made available, as SST is now collected through a satellite network, and catch and search data could be radioed in if the fishermen were willing to cooperate. Also, the real-time forecasts can be viewed as the best we can do; any delay in obtaining the data should only worsen the quality of the forecast.

As the model forecasts $LNCPUe(t)$, we used the unbiased inverse transform (Granger and Newbold 1977, p. 307):

$$CPUE(t) = \exp\{LNCPUe(t) + 0.5 \cdot (SE)^2\}$$

where SE is the standard error of the forecast on the logarithmic scale.

The forecasts for the years 1981 and 1982 give a reasonable fit to the observed data (Fig. 8). The amplitude and duration of the seasonal fluctuations are reasonably described. In 1981, when there were real SST data, the increase in CPUE at the beginning of the main cold season was anticipated by the model's forecast. In 1982, the forecast trailed by one period and was partly brought up by the increase in CPUE itself. As noted earlier, the estimated seasonal cycle for SST was used in place of the missing data in these periods, and it is likely that the seasonal cycle did not successfully capture the onset of the upwelling season that year. The actual fishing success responded to a real decrease in temperature, while the filled in data contained no change in SST that would predict a rise in CPUE. Based on the results for 1981 and the predictions for other years where real data were available, there are justifiable reasons to believe that with the proper SST data the model would have forecasted an increase in CPUE.

The model did a reasonable job of predicting the very high peaks in CPUE in 1981 and especially in 1982. This is particularly surprising, since the catch in 1982 had a sharp increase in the percentage of *S. aurita* found in the catch. Although further testing would still be needed, it does appear that this

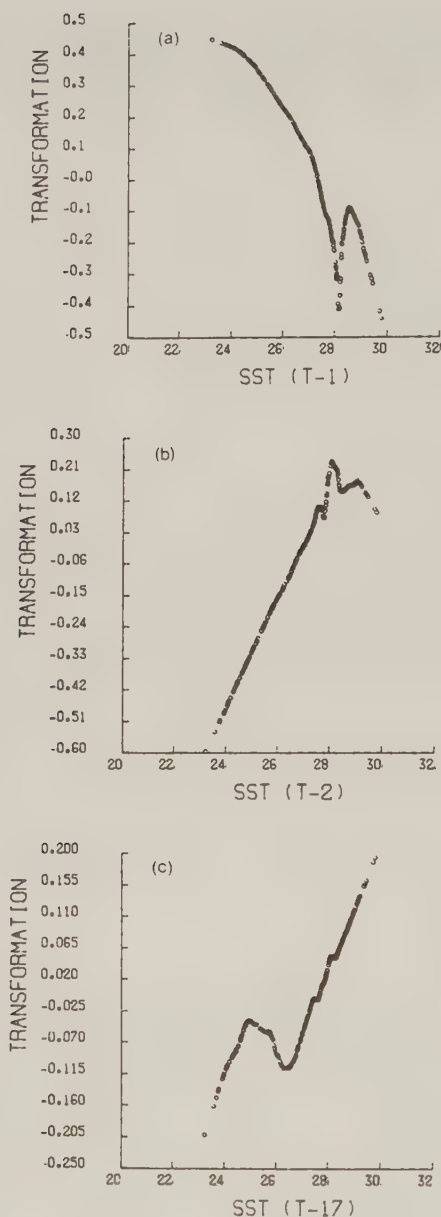


FIG. 7. Estimated optimal transformations of SST.

first-pass effort at modeling the dynamics could produce useful forecasts of the start and close of the fishing season and of the relative success in fishing that could be expected.

Discussion and Conclusions

The model estimated in this paper as well as the calculated transformations appear to provide a useful understanding of how the environment and past fishing success affect present fishing conditions. When good environmental data are available, the estimated model also provides a first-pass forecast that

may be able to predict the start and close of fishing seasons and to predict catch rates during this period.

We have chosen to model the combined CPUE over all the species. There is a trade-off in this decision. With CPUE combined over all the species, it is not possible to interpret the results in terms of the dynamics of an individual species. Different species may react in different ways to environmental events so that the combined result may not reflect either species' behavior accurately.

On the other hand, CPUE combined over all species is more reflective of the situation as viewed by the fishermen. Also, it is not clear how to partition the effort between species, so that any species-specific measure of CPUE may have more problems than a CPUE combined over species. Further, it is likely that all the species feed on similar food sources and respond to an increase in food availability in a similar fashion. If the main influence of the environment is due to its affect on food availability, then CPUE combined over all species should be a very reasonable measure.

There are several features of the data that need to be checked. Some of the data were "filled in" using a smoothing algorithm, and it is not desirable to have these data points unduly influence the analysis. Also, in 1982 there was a sharp change in species composition, with *S. aurita*, a species associated with colder waters, increasing dramatically over the other species which apparently do not have as strong a temperature preference.

The filled in data appear to have had little influence on the model estimation, but they significantly affected the model fit and especially the model forecasts. The CPUE data have relatively few missing data points, and these points are for the most part randomly scattered throughout the data set. Thus, the filled in CPUE values probably affected the analysis little. SST data are missing almost the entire year of 1969 and the last half of 1982. However, an almost identical model is estimated whether the years 1981 and 1982 are included or not and for either method of filling in the missing SST values. So the estimated model appears to be robust to these fill-ins.

The predicted and forecasted values, particularly for the end of 1982, appear to be affected by the filled in data. This is not surprising, as the model looks for a sharp change in SST to produce a sharp change in CPUE; the seasonal cycle of SST may not accurately reflect the timing of the onset of upwelling in 1982.

At a fortnightly time scale, the measure of CPUE used probably reflects the availability of the pelagic stocks more than it reflects the year-to-year abundance of the stocks. As discussed earlier, the model predicts strong persistence in CPUE, so that once fish are present they tend to remain. The "kick" to increase appears to be associated with a drop in temperature from two fortnights ago to one fortnight ago. This appears to be consistent with upwelling periods. The transformations suggest a strong linear effect between 22 and 27°C and then a dropoff between 28 and 29°C. This is consistent with a study of Marchal (1967) on a single year's data where he found that 23–26°C was the optimum temperature range. Binet (1976) has shown that increases in zooplankton abundance occur one fortnight after a drop in temperature, and the increase in zooplankton is strongest following the onset of upwelling. This is consistent with the interpretation of our model. The pelagic species probably come to the surface more and school more when there is abundant zooplankton biomass around which to aggregate.

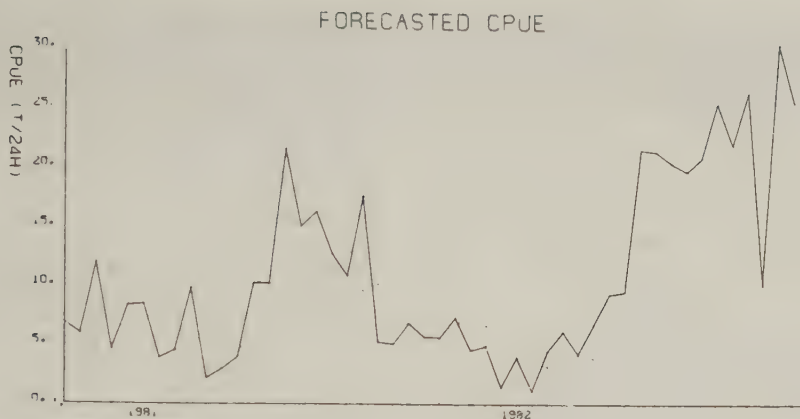


FIG. 8. Observed (solid line) and forecasted (broken line) CPUE in 1981 and 1982 per fortnight.

The CPUE of the coastal pelagic fish stocks off the Ivory Coast fluctuates greatly from one fortnight to another. Using multivariate time series methods, a model has been constructed which explains 43% of the variance in the original series and provides reasonable forecasts of future data. The estimated model has a nice biological interpretation which is consistent with past studies on these species. By finding appropriate transformations of the original series, a model can be constructed which explains almost 60% of the total variance in the CPUE series. These transformations clarify the threshold and other nonlinear effects between CPUE and the environment.

The present results suggest that, by themselves, variables such as SST or salinity are not sufficient to explain the evolution of CPUE, particularly when measured at the same time period as the catch. Moreover, there are other environmental variables such as wind or subsurface data that were not available for our study but might also be important predictors of CPUE (Bakun and Parrish (1980) presented a list of likely environmental variables). Our results suggest that the measured environmental variables act as surrogate variables for oceanographic and biological processes that create favorable conditions for the targeted fish species. Therefore, it is the dynamics of these variables between periods that are important, not a static value at any one time period. A similar result was found by Mendelssohn and Roy (1986) for tuna in the Gulf of Guinea.

Finally, although our techniques are empirical, we have shown that they lend themselves to identifying the underlying processes involved. The modeling approach also avoids the problems of just examining cross-correlations, which are not independent of cross-correlations at other lags or of autocorrelations in either series. This can lead to spurious conclusions about relationships and the lags at which they occur. We have also used a new technique for identifying the appropriate scale or form of the relationships between the different variables under consideration.

Acknowledgements

We wish to express our gratitude to the Centre de Recherche Oceanographique d'Abidjan who made this study possible. Support for one of the authors (P. Cury) was provided through a cooperative agreement between NMFS and ORSTOM during a visit to the Pacific Fisheries Environmental Group, Monterey, California. We thank

I. Barrett, A. Bakun, and J. R. Durand who made this visit possible. We are indebted to David Husby, Claude Roy, Remi Chuchla, and Denis Binet who helped us in different but complementary ways.

References

- AKAIKE, H., G. KITAGAWA, E. ARAHATA, AND F. TADA. 1979. TIMSAC-78, Computer Science Monographs No. 11. The Institute of Statistical Mathematics, Tokyo. 279 p.
- BAKUN, A., AND R. H. PARRISH. 1980. Environmental inputs to fishery population models for eastern boundary current regions, p. 67–104. In G. D. Sharp [ed.] Workshop on the effects of environmental variation on the survival of larval pelagic fishes. IOC Workshop Rep. 28.
- BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. U.K. Minist. Agric. Fish Food. Fish. Invest. (Ser. 2) 19: 533 p.
- BINET, D. 1976. Biovolumes et poids secs zooplanctoniques en relation avec le milieu pelagique au dessus du plateau ivoirien. Cah. ORSTOM Ser. Oceanogr. 14: 301–326.
- 1982. Influence des variations climatiques sur la pecherie des *Sardinella aurita* ivoiro-ganeennes: relation secheresse-surpeche. Oceanol. Acta 5: 443–452.
- 1983. Zooplankton des regions cotieres a upwellings saisonniers du golfe de Guinee. Cah. ORSTOM Ser. Oceanogr. 18: 357–380.
- BOUDREAU, F. R., J. NORMAND DUPONT, AND C. SYLVAIN. 1977. Modeles lineaires de prediction des débarquements de homard aux iles de la Madeleine (Golfe de Saint-Laurent). J. Fish. Res. Board Can. 34: 379–383.
- BREIMAN, L., AND J. H. FRIEDMAN. 1985. Estimating optimal transformations for multiple regression and correlation. J. Am. Stat. Assoc. 80: 580–619.
- CURY, P., AND C. ROY. 1985. Small pelagic fish abundance and upwelling off the Ivory Coast. Presented at UNESCO Symposium on vertical motions in the equatorial upper ocean and its effect upon living resources and the atmosphere, Paris, May 6–10.
- DEMPSTER, A. P., N. M. LAIRD, AND D. B. RUBIN. 1977. Maximum likelihood from incomplete data via the EM algorithm. J. R. Stat. Soc. Ser. B 39: 1–38.
- DIA, A. E. K. 1972. Etude de la nutrition de certains clupeides de Cote D'Ivoire. Projet de developpement de la peche pelagique cotiere, Ministere de la production animale. R/S 11/72: 33 p.
- EBERHARDT, L. L. 1970. Correlation, regression, and density dependence. Ecology 51: 306–310.
- FAO. 1974. Rapport terminal du projet FI: DP/IVC/66/506: Etude et mise en valeur des ressources en poissons pelagiques cotiers. Conclusions et recommandations. FAO, Rome. 72 p.
- FONTENEAU, A., AND E. G. MARCHAL. 1970. Recolte, stockage et traitement des donnees statistiques relatives a la peche des sardiniers (filet tournant) en Cote D'Ivoire. Doc. Sci. C.R.O. Abidjan. 1: 21–30.
- FOX, W. W. 1970. An exponential surplus yield model for optimizing exploited fish populations. Trans. Am. Fish. Soc. 99: 80–88.
- GRANGER, C. W. J., AND P. NEWBOLD. 1977. Forecasting economic time series. Economic theory and mathematical economics series. Academic

- Press. New York, NY. 333 p.
- JENKINS, G. M. 1979. Practical experiences with modelling and forecasting time series. Time Series Library. Gwilym Jenkins & Partners (overseas) Ltd., Jersey, Channel Islands. 146 p.
- MARCHAL, E. G. 1967. La peche des sardiniers ivoiriens en 1966. Doc. Sci. Prov. C.R.O. Abidjan. 19: 26 p.
- MENDELSSOHN, R. 1981. Using Box-Jenkins models to forecast fishery dynamics: identification, estimation, and checking. Fish. Bull. 78: 887-896.
- MENDELSSOHN, R., AND C. ROY. 1986. Environmental influences on the french, Ivory Coast, Senegalese and Moroccan tuna catches in the gulf of Guinea. In Special publication of the International Skipjack Year Program, ICCAT, Madrid.
- MORLIERE, A. 1970. Les saisons marines devant Abidjan. Doc. Sci. C.R.O. Abidjan. 1: 1-15.
- ORSTOM. 1976. Rapport du groupe de travail sur la sardinelle (*S. aurita*) des cotes ivoiro-ghanéennes. Fishery Research Unit Tema, Centre de Recherches Oceanographiques Abidjan, ORSTOM. 62 p.
- PARRISH, R. H., A. BAKUN, D. M. HUSBY, AND C. S. NELSON. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction, p. 731-777. In G. D. Sharp and J. Csirke [ed.] Proceedings of the Expert Consultation to examine changes in abundance and species of neritic fish resources. Costa Rica, 18-29 April 1983. FAO Fish. Rep. 291.
- PELLA, J. J., AND P. K. TOMLINSON. 1969. A generalized stock production model. Bull. IATTC 13: 419-496.
- PICAUT, J. 1983. Propagation of the seasonal upwelling in the eastern equatorial Atlantic. J. Phys. Oceanog. 13: 18-37.
1985. Major dynamics affecting the eastern tropical Atlantic and Pacific oceans. Calif. Coop. Oceanic Fish. Invest. Rep. 26: 41-50.
- RICKER, W. E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119: 300 p.
- SAILA, S. B., M. WIGBOUT, AND R. J. LERMIT. 1980. Comparison of some time series models for the analysis of fisheries data. J. Cons. Int. Explor. Mer 39: 44-52.
- SCHAEFER, M. B. 1954. Some aspects of the dynamics of population important to the management of the commercial marine fisheries. Bull. Int. Am. Trop. Tuna Comm. 1: 26-56.
- SHUMWAY, R. H., AND D. S. STOFFER. 1982. An approach to time series smoothing and forecasting using the EM algorithm. J. Time Ser. Anal. 3: 253-264.
- TIAO, G. C., AND G. E. P. BOX. 1981. Modeling multiple time series with applications. J. Am. Stat. Assoc. 76: 802-816.
- TIAO, G. C., G. E. P. BOX, M. R. GRUPE, G. B. HUDAK, W. R. BELL, AND I. CHANG. 1980. The Wisconsin multiple time series (WMTS-1) program. A preliminary guide. Department of Statistics, University of Wisconsin, Madison, WI. 75 p.

Appendix

Shumway-Stoffer Missing Data Algorithm

The Shumway-Stoffer (1982) missing data algorithm calculates maximum likelihood estimates of the parameters of the following state-space model:

$$\begin{aligned}x(t) &= Ax(t-1) + e(t) \\ y(t) &= Hx(t) + w(t)\end{aligned}$$

where $x(t)$ is an underlying state of the system at time t , A is a matrix of parameters to be estimated relating the underlying

state at time t to that at time $t-1$, $e(t)$ is the process error vector, $y(t)$ is the observed process at time t , H is a known matrix relating the underlying and observed processes, and $w(t)$ is a random vector, the observation error. The algorithm not only calculates maximum likelihood estimates of the parameters in the matrix A , but also calculates minimum mean-square error estimates of the underlying state $x(t)$, which is only observed with error in $y(t)$.

The algorithm has been extended to allow for missing data (i.e. missing components in the $y(t)$ vector), and the given reference shows how to put a multivariate autoregressive model into the required state-space form. The algorithm is a variant of the E-M algorithm of Dempster et al. (1977) and briefly proceeds as follows. For any estimate of the parameters, the algorithm uses a form of the Kalman filter to calculate the likelihood for that set of parameters. Minimum mean-square error estimates of the state vector $x(t)$ are then estimated using a slightly modified version of the Kalman fixed-interval smoothing algorithm. The new parameter estimates are then calculated by what is a regression-like equation. The next iteration then begins. The algorithm stops when the parameters have converged sufficiently.

For the applications in this paper, for example, the vector $y(t)$ is the observed CPUE in areas 4-7, the underlying state $x(t)$ is the "true" CPUE or density in areas 4-7 and the matrix A contains the parameters of a second-order autoregressive process. For the SST data, a second-order autoregressive process was estimated for each pair of bordering north-south areas.

Alternating Conditional Expectation (ACE) Algorithm

The ACE algorithm of Breiman and Friedman (1985) is an algorithm that estimates optimal transformations of variables in regression-like equations. The algorithm operates on the observation that for any given empirical transformations of the data, if we fix the values of all but one variable and solve the problem of what new transformation will minimize the normalized residual sum-of-squares, then the solution is a conditional expectation that can be empirically estimated using a smoothing algorithm.

The algorithm starts with the given variables and then alternately estimates the conditional expectations that would be derived from fixing all but one variable in turn. Hence, the name of the algorithm. The algorithm terminates when the changes in the estimated transformations are sufficiently small. The algorithm does not produce a given equation, but rather an empirical transformation of each data point for each variable. The shape of the transformation is found by plotting the transformed values of a variable versus the original values.

DISTRIBUTION AND YIELD OF THE DEEPWATER SHRIMP *HETEROCARPUS* RESOURCE IN THE MARIANAS

ROBERT B. MOFFITT AND JEFFREY J. POLOVINA¹

ABSTRACT

A shrimp trapping survey was conducted at 22 islands and banks in the Mariana Archipelago during a 2-year field period. Three species of deepwater shrimp were found in abundance at various depths: *Heterocarpus ensifer* at 366-550 m, *H. laevigatus* at 550-915 m, *H. longirostris* >915 m. *Heterocarpus laevigatus* was the largest and most abundant of the three and has the greatest economic potential. Estimates of the unexploited biomass of this species by bank were calculated from estimates of catchability, relative abundance, and habitat area. An archipelago average of the unexploited trappable biomass was estimated to be 0.8 t/nmi². Evaluation of length-frequency distributions produced estimates of asymptotic length (L_{∞}) of 55 mm carapace length, instantaneous growth constant (K) of 0.3 yr⁻¹, and instantaneous total mortality (Z) of 0.75 yr⁻¹. A recommended yield of 162.0 t/year (0.2 t/nmi² per year) for the entire archipelago was calculated using the Beverton and Holt yield-per-recruit equation based on minimum spawning stock considerations. Of this yield, 85% would come from the southern islands (e.g., Guam and Saipan), 13% from the northern islands (e.g., Pagan and Anatahan), and 2% from the western seamounts (e.g., Arakane Reef and Pathfinder Reef).

The Mariana Archipelago in the western Pacific Ocean stretches from Guam in the south at lat. 13°N to Farallon de Pajaros (also called Uracas) in the north at lat. 20°N (Fig. 1). Within the approximately 270,000 nmi² area of the 200 mi zone around the archipelago are two political entities—the Territory of Guam and the Commonwealth of the Northern Mariana Islands (CNMI)—and three geological formations—the southern island chain, the northern island chain, and the western seamount chain (Karig 1971). The purpose of this study was to assess the standing stock and sustainable yield of the deep-water pandalid shrimp resources in the Marianas.

Pandalid shrimp catches account for about 9% of the world shrimp landings or about 155,000 t in 1982 (FAO 1984). About 98% of this catch is of a few species of the genus *Pandalus* trawled at depths of 70-240 m in the cold-water areas of the North Atlantic, North Pacific, and Bering Sea. The next largest pandalid fishery is the trawl fishery for *Heterocarpus reedi* conducted at depths of 155-424 m in the waters off Chili and Peru (Holthuis 1980). The landings from this fishery were 3,450 t in 1982 (FAO 1984). In recent years, pandalid shrimp resources with commercial potential have been identified from deepwater trapping surveys conducted at depths of

200-1,200 m in the central and western Pacific (Clarke 1972; Wilder 1977; King 1980, 1981a, 1981b; Moffitt 1983). The primary component of these catches has been species of the genus *Heterocarpus*, including *H. laevigatus*, *H. ensifer*, *H. sibogae*, *H. longirostris*, and *H. gibbosus*. Trawling for these species has produced poor results (Struhsaker and Yoshida 1975) which may be due to the depths involved, the rough bottom surrounding the Pacific islands, or behavioral characteristics of the shrimp. In Hawaii a rapidly expanding commercial trap fishery has been established with 1983 annual landings of about 135 t. Catches of 1,350 t have been projected for the near future by the Western Pacific Regional Fishery Management Council (WPRFMC 1984). This projected yield has not materialized and does not appear to be forthcoming since the larger shrimp trapping vessels have left the fishery for economic reasons. Commercial ventures in Guam and the CNMI have been sporadic and short lived; landings of 0.3 t were reported in 1982, the last year that the resource was fished.²

SAMPLING GEAR AND METHODS

Shrimp trapping operations in the Mariana Archi-

¹Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

²Western Pacific Fishery Information Network data on file at the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

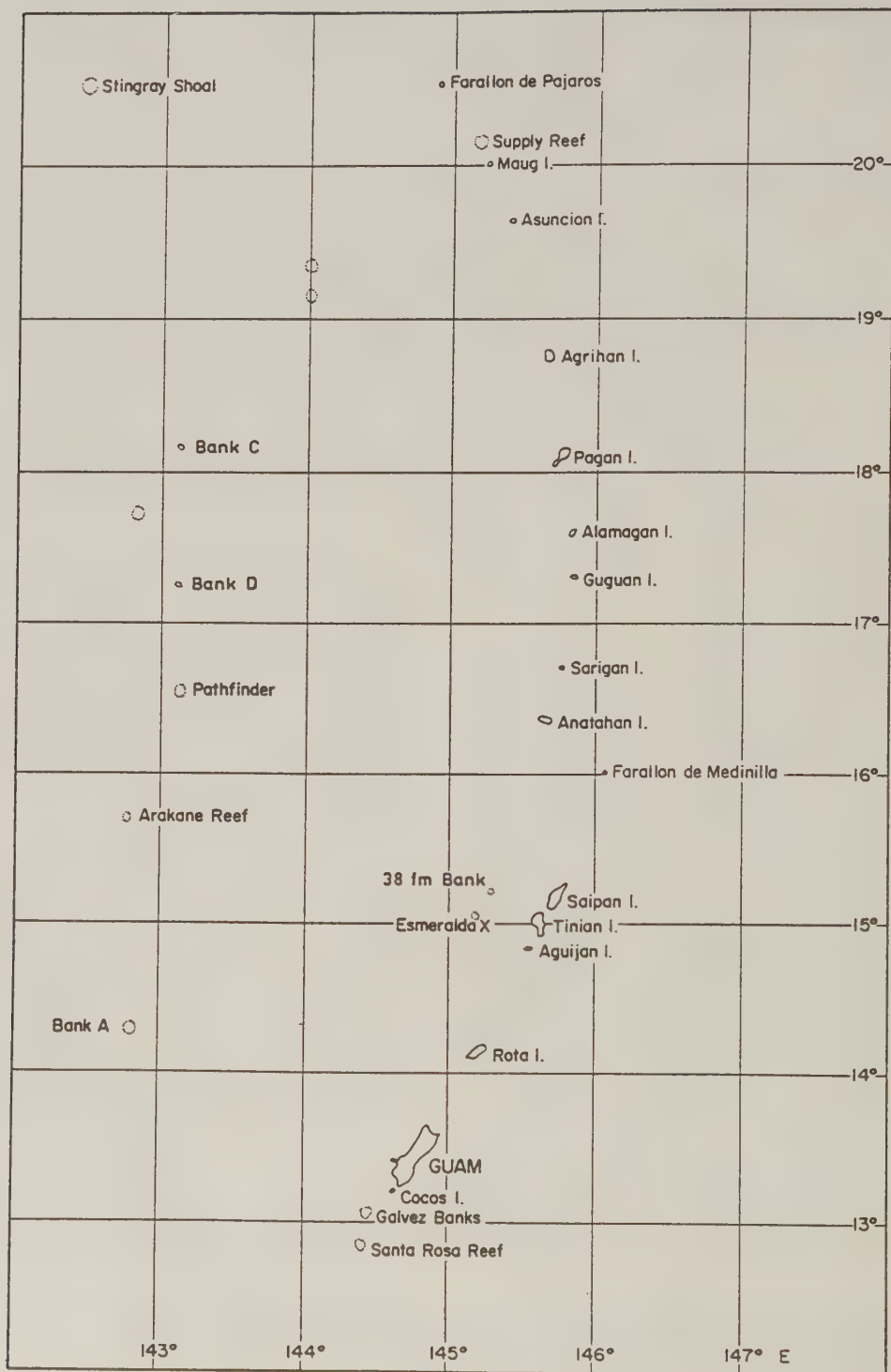


FIGURE 1.—Chart of the Mariana Archipelago.

pelago were conducted on seven cruises of the NOAA ship *Townsend Cromwell* (TC) between April 1982 and August 1984 and one charter cruise of the University of Guam vessel *Pesquedot* (PQ) in August 1984. The standard gear used consisted of strings of five canvas-covered, half-round shrimp traps set about 40 m apart. The traps were constructed of a reinforcing bar frame (about 90 cm long, 65 cm wide, and 45 cm high) wrapped with 2.5×1.3 cm mesh, 18-gauge welded wire. An entry cone with an opening of approximately 10 cm was located at each end of the trap. A figure of this general trap design is shown in Gooding (1984). The ground lines attaching the traps together and the main lines attaching the ground line to the surface buoys were of 13 mm polypropylene line. Strings were usually set in the afternoon and retrieved the following morning. Normal soaking times ranged from 15 to 24 hours. Traps were baited with Pacific mackerel, *Scomber japonicus*.

Ordinarily, subsamples of 100 specimens of each of the three major species of *Heterocarpus* (*H. laevigatus*, *H. ensifer*, and *H. longirostris*) were saved each day from each depth sampled. Two sampling sites, Esmeralda Bank and Pagan Island, were visited on each of six *Cromwell* cruises and large subsamples of 400 *H. laevigatus* were saved on each visit. All specimens were returned to the laboratory where the carapace length, sex, and reproductive condition were recorded. The areas of suitable habitat for *H. laevigatus* at each island and bank location was estimated from charts using a computer aided planimeter.

In this study, the yield assessment approach described by Polovina and Ralston (1986) was employed. A systematic survey of 22 islands and banks gave information on the depth range of the primary species and their relative abundance by area. An intensive fishing experiment produced an estimate of catchability using the Leslie method (Ralston 1986). This information combined with an estimate of the area of suitable habitat for each island or bank was used to estimate available biomass by location. Estimates of growth were obtained by application of Elefan I (Pauly 1982) to a site specific time series of length-frequency data. The ratio of mortality to growth and asymptotic length was estimated from a large length-frequency sample (Wetherall et al. in press). Equilibrium yield as a function of fishing mortality was determined from the Beverton and Holt (1956) yield-per-recruit equation as the product of yield per unexploited trappable biomass and the trappable recruited biomass estimate obtained from the systematic sampling and intensive fishing (Polo-

vina and Ralston 1986). Estimates of recommended yield from the equilibrium yield equation were obtained based on marginal yield and minimum spawning stock biomass considerations.

RESULTS³

Throughout the course of this survey a total effort of 2,508 trap-nights was expended at 527 shrimp trapping stations. The total catch of pandalid shrimp was 5,188 kg for an overall catch rate of 2.07 kg/trap-night. Over 99% of this catch was composed of *H. ensifer*, *H. laevigatus*, and *H. longirostris*. A complete list of shrimp species taken during this study is given in Table 1.

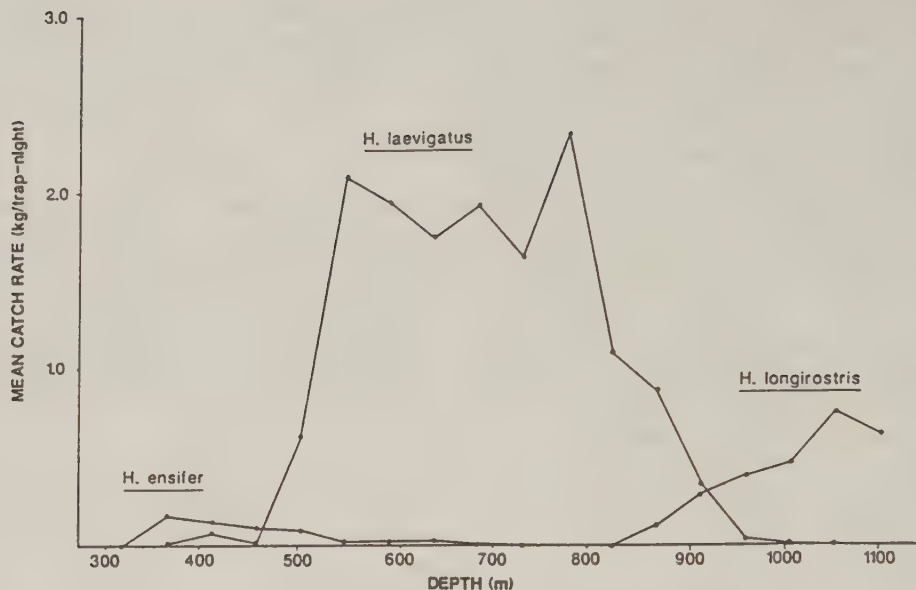
TABLE 1.—List of shrimp species taken (C = common, F = frequent, R = rare).

Species	Frequency	Depth of abundance (m)
Pandalidae		
<i>Plesionika serratifrons</i>	C	90-270
<i>Plesionika longirostris</i>	C	180-360
<i>Plesionika ensis</i>	F	450-630
<i>Plesionika maria</i>	R	360-450
<i>Heterocarpus ensifer</i>	C	360-540
<i>Heterocarpus gibbosus</i>	R	360-450
<i>Heterocarpus sibogae</i>	R	630
<i>Heterocarpus lepidus</i>	F	540-720
<i>Heterocarpus laevigatus</i>	C	540-810
<i>Heterocarpus dorsalis</i>	F	630-900
<i>Heterocarpus longirostris</i>	C	>900
<i>Heterocarpus tricarinatus</i>	R	900
Oplophoridae		
<i>Acanthephyra eximia</i>	F	810-990
Aristaeidae		
<i>Plesiopenaeus edwardsianus</i>	R	630-810

DEPTH AND SIZE DISTRIBUTION

A plot of catch per unit effort (CPUE) versus depth for the three major species (Fig. 2) shows that they inhabit different depth strata. *Heterocarpus ensifer* is the shallowest dwelling of these species. The maximum catch rate for this species was 0.17 kg/trap-night at a depth of 366 m (200 fathoms). Unfortunately, 366 m was the shallowest depth targeted throughout most of the survey. A small amount of effort was expended in the 137-274 m (75-150 fathoms) depth range on cruises TC-84-02 and PQ-84-01. *Heterocarpus ensifer* catches in this depth range were negligible (only five shrimp in 37 trap-nights). *Heterocarpus laevigatus*, the most abundant shrimp taken in our survey, was caught

³Portions of this section are also presented in Polovina et al. 1985.

FIGURE 2.—Catch rate of three species of *Heterocarpus* by depth.

in large numbers at depths between 549 and 777 m (300 and 425 fathoms). A maximum catch rate of 2.33 kg/trap-night was obtained at 777 m. *Heterocarpus longirostris* was the deepest dwelling of the *Heterocarpus* species taken, ranging from 823 m (450 fathoms) down past 1,097 m (600 fathoms), which was the greatest depth targeted in this study. Maximum catch rates of *H. longirostris* were obtained at 1,052 m (575 fathoms), but the deeper end of this species' range was not sampled and, as with *H. ensifer*, it is uncertain that the depth of maximum catch rate obtained here is indicative of depth of maximum abundance.

Heterocarpus ensifer was the smallest of the three major species taken. Carapace lengths of 3,401 individuals ranged from 11 to 38 mm with a mean of 26.4 mm. *Heterocarpus laevigatus* was the largest species taken. The mean carapace length was 38.2 mm and the range was 13 to 61 mm ($N = 16,405$). The mean carapace length of *H. longirostris* was similar to that of *H. laevigatus* ($\bar{x} = 37.5$ mm), but the size range of 1,443 individuals was more restricted (20 to 50 mm). The mean size of *H. longirostris* taken in this study is probably higher than the mean of catchable shrimp of this species for all depths. We set traps only in the shallower end of this species' depth range (<1,143 m) where the population is dominated by females that grow to a larger size than the males.

It has been suggested that the size of shrimp

varies with depth, i.e., larger shrimp occur within the range of maximum abundance while smaller individuals were found in shallower or deeper water (Clarke 1972; Wilder 1977). This type of distribution was not observed for any of the three major species of *Heterocarpus* in the Marianas. Linear regressions of mean carapace length with depth by sex were computed for each of the three species. A significant decrease in carapace length with increasing depth was obtained for *H. longirostris* females, although the full depth range of this species was not sampled. In all other cases, no significant change in size with depth was observed (Table 2).

Wilder (1977) reported high male to female ratios of 3-4 to 1 for *H. ensifer* and *H. laevigatus* taken around Guam. He also stated that small individuals were nearly all males and large individuals almost all female. This was not true for the shrimp examined in this study. The overall sex ratios (ex-

TABLE 2.—Results of mean carapace length by depth regressions for three species of *Heterocarpus* by sex.

Species	Sex	Regression coefficient	R^2	Probability
<i>H. ensifer</i>	Male	0.008	0.41	0.06
	Female	0.002	0.03	0.64
<i>H. laevigatus</i>	Male	-0.007	0.26	0.06
	Female	-0.017	0.16	0.16
<i>H. longirostris</i>	Male	-0.004	0.02	0.83
	Female	-0.04	0.67	0.02

pressed in percent males) for the three major species were 52.8% for *H. ensifer* ($N = 3,302$), 55.2% for *H. laevigatus* ($N = 12,555$), and 24.2% for *H. longirostris* ($N = 1,408$). These ratios tended to hold true for all size classes except the very largest of each species which were indeed nearly all females. Sex ratios did differ by depth showing that the two sexes tend to occupy different areas. In all three major species, females were more abundant at the shallower end of the depth range and males at the deeper end (Fig. 3). This relationship is much more obvious for *H. laevigatus* and *H. longirostris* than for *H. ensifer*. For *H. longirostris*, this may explain the small percentage of males taken in this study since the deeper end of the depth range of this species was not sampled.

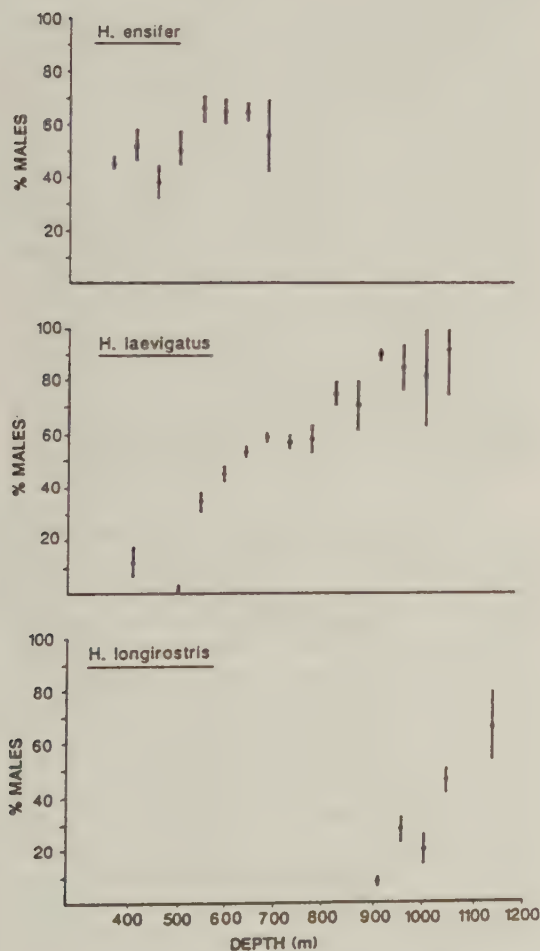


FIGURE 3.—Sex ratio by depth for three species of *Heterocarpus* with 95% confidence limits.

REPRODUCTION

Pandalid shrimp are typically considered to be protandrous hermaphrodites. This is indeed the case for the *Pandalus* species taken in the subarctic areas (Butler 1964). In these species the shrimp spend the first few years of life as functional males, transforming into functional females for the last year or two of life. Clarke (1972) and Wilder (1977) suggested that the tropical *Heterocarpus* shrimp also are protandrous hermaphrodites. The sex ratios obtained in our studies, particularly the near even ratio for the smaller individuals led us to believe that this was not the case. King and Moffitt (1984) examined males of several species of *Heterocarpus* and *Plesionika* for relative growth of the appendix masculina on the second pleopod (a secondary sex characteristic). If these species were indeed protandrous hermaphrodites, the relative size of the male appendage should decrease with increasing carapace length (as the shrimp transforms from male to female). This was not so for any of the tropical pandalids examined. Instead, the relative size of the male appendage increased with increased carapace length indicating maturation as a male. The Marianas data for the ratio (R) of the appendix masculina to the appendix interna versus carapace length (CL) was fit to the logistic model with three parameters, a , b , and c (Gunderson et al. 1980). Table 3 lists the parameters obtained when fitted to the model

$$R \times 100 = \frac{a}{1 + e^{-b(CL-c)}}$$

The fit to the nonlinear regression for *H. longirostris* was not particularly good due to the lack of small males in our collection. When the data for this species are fit to a linear regression, however, the slope of the regression is positive indicating relative growth of the secondary sexual characteristics

TABLE 3.—Parameter values for the nonlinear regression of the relative length of the appendix masculina versus carapace length.

Species	a^1	b	c^2
<i>Plesionika longirostris</i>	106.83	0.75	11.67
<i>Heterocarpus ensifer</i>	80.35	0.43	15.05
<i>Heterocarpus laevigatus</i>	104.97	0.29	28.09
<i>Heterocarpus longirostris</i>	158.32	0.05	19.36

¹Asymptotic value for the ratio of the lengths of the appendix masculina and the appendix interna.

²Carapace length at the inflection point at 50% of the asymptotic ratio.

with increasing size (regression coefficient = 1.64, $r^2 = 0.52$).

Based on the assumption that the relative growth of the appendix masculina correlates directly with maturity, we chose the point where this appendage is 90% of its asymptotic value to define the length at maturity for males. The 90% level was used instead of 50% of the asymptotic value, as used for the females below, because the 50% point would be where the males are 50% mature, not where 50% of the males are mature. Using this definition, the carapace length at maturity (L_M) for males of *H. ensifer* is 20.2 mm and that of *H. laevigatus* is 35.7 mm. For *H. longirostris*, the length at maturity is estimated at 31 mm.

The length at maturity of females is perhaps more important in assessment work since the females are directly responsible for the production of recruits to the population. For this study we used the presence of eggs (berried) as the indicator of maturity. The length at maturity is defined as the size where 50% of the females are mature (Gunderson et al. 1980). When using the presence of eggs as the measure of maturity, the sample must be restricted to females collected during the time of year that egg bearing can be expected. For *H. laevigatus*, the breeding season is relatively discrete (November to February), whereas for *H. ensifer* and *H. longirostris* there are peaks in December and May (Fig. 4). Data for each species were fitted to the same non-linear regression model used for the males. Asymptotic values for percent berried by carapace length are 66% for *H. ensifer*, 92% for *H. laevigatus*, and 55% for *H. longirostris*. The carapace lengths associated with values equal to one-half of the asymptotic values are the L_M for the various species. These are 23.9 mm for *H. ensifer*, 42.7 mm for *H. laevigatus*, and 37.4 mm for *H. longirostris*.

YIELD ASSESSMENT

The assumptions and methods of yield assessment used in this study are presented in Polovina and Ralston (1986) and Wetherall et al. (in press). Because *H. laevigatus* yielded the highest catch rates and because it is generally regarded as having superior market acceptability, most of our fishing effort targeted this species. Hence estimates of total biomass and sustainable yield for the pandalid resource are restricted to this species.

GROWTH AND MORTALITY

Estimates of asymptotic size (L_∞) and the ratio

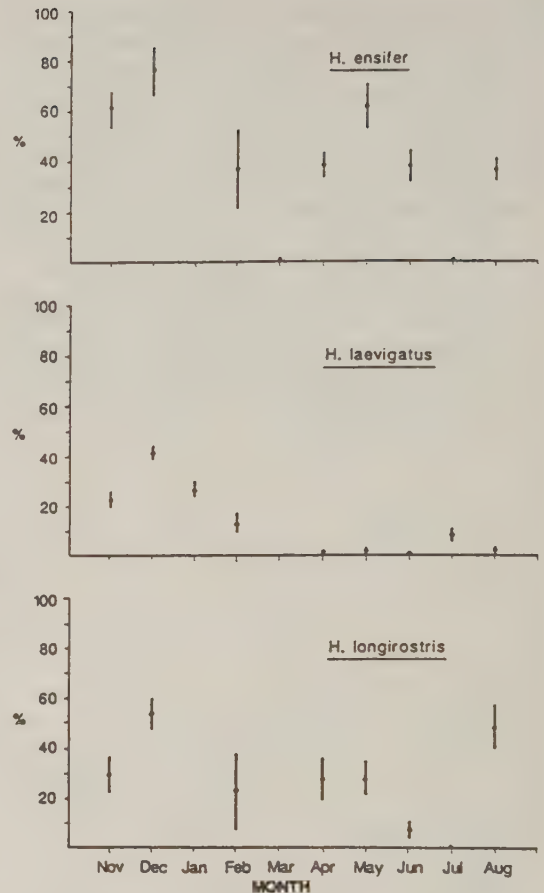


FIGURE 4.—Percentage of females bearing eggs by month for three species of *Heterocarpus* with 95% confidence limits.

of instantaneous total mortality to the instantaneous growth constant (Z/K) were obtained by examining the descending limb of the length-frequency distribution using the regression method based on the Beverton and Holt (1956) model (Wetherall et al. in press). Table 4 lists the values of L_∞ and Z/K for males, females, and pooled sexes for each of the three major species. As anticipated, L_∞ values for females are larger than those for males of the same species. Estimates of length at recruitment to the exploitable population (L_R) were obtained by applying the method of Gulland (1969) to the ascending limb of the same length-frequency distributions. *Heterocarpus ensifer* is recruited into the fishery at a carapace length of 23 mm, *H. laevigatus* at 29 mm, and *H. longirostris* at 34 mm.

By fixing the L_∞ value at the estimates obtained from the large length-frequency sample and using

TABLE 4.— L_{∞} and Z/K estimates for the three major species of *Heterocarpus* by sex from length-frequency data.

Species	L_{∞}	Z/K
<i>Heterocarpus ensifer</i>		
Males	34.5	2.6
Females	37.5	3.0
Sexes combined	36.6	2.9
<i>Heterocarpus laevigatus</i>		
Males	51.3	2.1
Females	55.4	1.9
Sexes combined	55.2	2.5
<i>Heterocarpus longirostris</i>		
Males	41.0	1.7
Females	48.1	1.9
Sexes combined	48.6	2.2

Elefan I (Pauly 1982) to fit the von Bertalanffy growth curve to the time series data for *H. laevigatus* collected at Esmeralda Bank and Pagan Island, the growth constant K can be estimated. When applied to the sexes separately, multiple estimates were obtained for each category ranging from 0.19 to 0.31 yr⁻¹. The inconsistency of these estimates within area and sex groupings was most likely due to the small sample size. When sexes were pooled, however, K was estimated at 0.30 yr⁻¹ for both areas. Estimates of the age at recruitment and maturity were obtained by solving the von Bertalanffy equation for the particular carapace lengths estimated above. For female *H. laevigatus*, with a $L_R = 29$ mm, the $T_R = 2.0$ years, and with $L_M = 43$ mm, the $T_M = 4.5$ years. With a K estimate of 0.3 yr⁻¹ and Z/K of 2.5, an estimate for Z of 0.75 yr⁻¹ is obtained. Because there is no fishery for *H. laevigatus* in the Marianas, Z is equivalent to natural mortality (M).

UNEXPLOITED BIOMASS

Because standard trapping techniques were used throughout our study, CPUE values from various locations could be used as a measure of relative abundance. The unexploited biomass of the *H. laevigatus* resource for each area is then calculated as the product of the area of suitable habitat and relative abundance divided by the coefficient of catchability ($q = 0.001945$ trap-night⁻¹) estimated from the Alamagan Island intensive trapping operation (Ralston 1986). Although the catch rate from the western seamounts is about twice that of the southern island chain, the fiftyfold greater area of suitable habitat around the southern islands more than compensates for the low catch rates in producing a higher biomass estimate for the southern islands (Table 5).

TABLE 5.—Catch rates, habitat areas, and unexploited biomass estimates for *Heterocarpus laevigatus* by location.

	Catch rate (kg/trap-night)	Area (nmi ²)	Biomass (t)
Northern Banks			
Maug	1.88	3.83	3.7
Asuncion	2.11	5.93	6.4
Agrihan	1.96	12.39	12.5
Pagan	2.17	16.19	18.0
Alamagan	2.18	11.43	12.8
Guguan	2.52	5.60	7.2
Sarigan	1.45	4.55	3.4
Anatahan	2.36	10.89	13.2
38 Fathom Bank	2.12	6.37	6.9
Esmeralda Bank	1.35	2.03	1.4
Mean =	2.01	Total = 79.21	85.5
Southern Banks			
Farallon de			
Medinilla	0.97	88.55	44.2
Saipan	2.06	213.99	226.5
Tinian	1.81	73.80	68.4
Aguijan	1.61	39.36	32.6
Rota	1.02	197.31	103.6
Guam	0.48	44.24	16.2
Galvez and			
Santa Rosa	1.78	50.77	84.5
Mean =	1.39	Total = 708.02	576.0
Seamounts			
Bank C	2.07	2.71	2.9
Bank D	2.72	2.71	3.8
Pathfinder	2.79	2.71	3.9
Arakane	2.83	2.10	2.1
Bank A	1.43	3.33	2.4
Mean =	2.37	Total = 13.56	15.1

EQUILIBRIUM YIELD

With the values for K , L_{∞} , M , and T_R , the Beverton and Holt yield-per-recruit equation can be used to compute the ratio of equilibrium yield to unexploited recruited biomass (Y/B) as a function of fishing mortality (F) (Polovina and Ralston 1986). Because the shrimp resource in the Marianas is not fished, the estimates of the biomass for each bank represent the unexploited trappable biomass (B), and hence, the product of Y/B and B gives the equilibrium yield as a function of F (Table 6). As F increases, the equilibrium yield increases rapidly for low levels of F . The relationship between F and the equilibrium yield estimated from the Beverton and Holt yield-per-recruit equation assumes that recruitment is unchanged as F increases and does not take into account any economic considerations. Ideally a spawner-recruit relationship is needed to account for changes in yield because of the changes in recruitment which might occur as F increases. However, in the absence of a knowledge of the spawner-recruit curve, two approaches can be used to estimate recommended yield. One approach esti-

TABLE 6.—Equilibrium yield of *Heterocarpus laevigatus* and relative spawning stock biomass as a function of fishing mortality (F).

F	Total yield (t)	Relative spawning stock biomass
0.1	56.2	0.70
0.2	95.6	0.51
0.3	124.2	0.37
0.4	145.4	0.27
0.5	161.6	0.20
0.6	174.1	0.15
0.7	184.1	0.11
0.8	192.0	0.09
0.9	198.5	0.07
1.0	203.8	0.05

mates the recommended yield from the yield-per-recruit derived yield equation as the yield which corresponds to that level of effort where an increase in one unit of effort will increase the catch by 0.1 of the amount caught by the very first unit of effort (Gulland 1983, 1984). This effort is denoted as $F_{0.1}$ and the corresponding yield as $Y_{0.1}$. The value of $F_{0.1}$ for *H. laevigatus* in the Marianas is 0.8 and $Y_{0.1}$ is 192 t annually (Table 6) from areas within the depth range of 500-825 m.

A second approach to estimate recommended yield uses a computation of the spawning stock biomass. With an age estimate of the onset of sexual maturity, the spawning stock biomass for a level of F relative to the spawning stock biomass, in the absence of fishing, can be computed from the Beverton and Holt yield-per-recruit equation (Polovina and Ralston 1986). This relative spawning stock biomass can be used to determine the maximum value of F before a substantial decline in recruitment occurs. The recommended yield can then be estimated as the yield from the constant recruitment yield curve which corresponds to that maximum value of F . This is a conservative approach because it does not incorporate any density dependent compensation, i.e., size at onset of sexual maturity does not decrease as density decreases. The relationship between the relative spawning stock biomass and recruitment is not known for *H. laevigatus*, but it has been suggested that as a lower bound the relative spawning stock biomass should not be reduced below 20% of the unexploited level if a substantial reduction in recruitment is to be avoided (Beddington and Cooke 1983). When F is 0.5, the relative spawning stock biomass is estimated to be 20% of the unexploited level, and the equilibrium yield at this level of fishing is estimated at 162 t annually (Table 6) for the depth range of 500-825 m. To be conservative, the lower yield estimate of 162 t annually from the Mariana

Archipelago will be used. Given the habitat area from 500 to 825 m, this yield is equivalent to 0.20 t/nmi². An approximate variance for this yield, and hence an approximate confidence interval, can be computed from a Taylor series expansion of the yield estimator if it is assumed that the variance of the yield estimate is due primarily to variances in bank CPUE and catchability. The yield at each bank is computed as

$$\text{Yield} = (\text{CPUE}/q)(\text{Area})(Y/B).$$

Thus the variance of the yield ($V(\text{Yield})$) can be expressed as

$$\begin{aligned} V(\text{Yield}) &= (\text{Area})^2 (Y/B)^2 V(\text{CPUE}/q), \\ &= (\text{Area})^2 (Y/B)^2 \\ &\quad \times \left[\frac{V(\text{CPUE})}{q^2} + \frac{(\text{CPUE})^2 V(q)}{q^4} \right]. \end{aligned}$$

Estimates of $V(\text{CPUE})$ were obtained from the repeat sampling at each bank and ranged from 0.02 at Guam to 0.64 at Sarigan, while $V(q)$, estimated at 5.5×10^{-7} , was obtained from the intensive trapping work. The variance of the total yield was estimated as the sum of the individual bank variance. The 95% confidence interval, derived from the estimate ± 1.96 times the standard deviation of the estimate of total yield, resulted in a targeted yield range of 102 to 218 t (0.12 to 0.27 t/nmi²) per year. About 85% of this yield would come from the southern islands and banks, 13% from the northern islands, and about 2% from the western seamounts (Table 7).

DISCUSSION

Although trap design, depth fished, and species present undoubtedly affect catch rate, catch rates reported in other studies using differing trap designs in various areas fall within a fairly tight range of 1.2 to 6.6 kg/trap-night (Table 8). This indicates that the productivity of deepwater pandalids is relatively uniform throughout the tropical central and western Pacific, and the first estimate of recommended yield of 0.2 t/nmi² obtained from the Mariana Archipelago can be applied to other Pacific islands, though the relative importance of the various species may differ greatly from area to area.

In our study *H. ensifer*, *H. laevigatus*, and *H.*

TABLE 7.—Equilibrium yield for *Heterocarpus* shrimps in the 500-825 m depth range for a fishing mortality of 0.5.

Bank	Yield (t/yr)
Northern Banks	
Maug	0.9
Asuncion	1.5
Agrihan	3.0
Pagan	4.3
Alamagan	3.0
Guguan	1.7
Sarigan	0.8
Anatahan	3.1
38 Fathom	1.7
Esmeralda	0.3
Total	20.3
Southern Banks	
Farallon de Medinilla	10.6
Saipan	54.1
Tinian	16.3
Aguijan	7.8
Rota	24.7
Guam	3.9
Galvez and Santa Rosa	20.2
Total	137.6
Seamounts	
Bank C	0.7
Bank D	0.9
Pathfinder	0.9
Arakane	0.5
Bank A	0.6
Total	3.6
Archipelago total	161.5

TABLE 8.—Catch rates of pandalid shrimp in the tropical Pacific.

Area	Catch rate (kg/trap-night)	Source
Tonga	1.2	King 1981b
Samoa	1.4	King 1980
Fiji	1.5	King 1983
Hawaii (main islands)	1.5	Clarke 1972
Guam	2.1	Wilder 1977
Mariana Archipelago	2.1	Present study
Hawaii (NWHI)	2.5-3.5	Oishi 1983
Vanuatu	2.8	King 1981a
Hawaii (main islands)	3.5-5.0	Hawaiian Divers, Inc. 1983 (text fn. 4)
Hawaii (main islands)	6.6	Struhsaker and Aasted 1974

longirostris proved to be the major components of the catch within their respective depth zones. *Heterocarpus ensifer* was the shallowest dwelling and the least abundant of the three major species in the Marianas. Its range of abundance was 366 to 503 m (200 to 275 fathoms) and the peak catch rate was 0.17 kg/trap-night at 366 m. In Hawaii, *H. ensifer* appears to be the most abundant species. Average catch rates are between 1.5 and 6.6 kg/trap-night in a somewhat wider reported depth

of abundance of 274 to 600 m (Clarke 1972; Struhsaker and Aasted 1974; Gooding 1984). In the Southern Hemisphere, *H. ensifer* is not found in great abundance and is replaced in the 300 to 500 m depth range by a very closely related species, *H. sibogae* (King 1983).

Heterocarpus laevigatus is an important part of the catch throughout the central and western Pacific. In the Marianas, this was the most common species. Its abundance peaked between 549 and 777 m (300 and 425 fathoms) and the maximum catch rate of 2.33 kg/trap-night was obtained at 777 m. In the Northwestern Hawaiian Islands (NWHI), the same standard half-round traps caught just under 1.0 kg/trap-night in an optimum depth range of 500 to 800 m (Gooding 1984). Commercial vessels using larger traps obtained catches of 2.5 to 5.0 kg/trap-night in the Hawaii area and found that the optimum depth range is shallower in the main Hawaiian Islands (530 to 622 m) than in the NWHI (640 to 732 m) (Hawaiian Divers 1983⁴; Oishi 1983; Gooding 1984). In the South Pacific, *H. laevigatus* is reported to be abundant at depths of 549 to 640 m and catch rates range from 0.4 to 1.1 kg/trap-night depending on the area studied (King 1983).

Before this study, *H. longirostris* had been known to science from only four specimens taken in the Indian Ocean (Moffitt 1983). In the Marianas, it occurs in sufficient quantity to suggest a commercial potential. *Heterocarpus longirostris* is probably present in many other areas in the Pacific but has not been found because its optimum depth range is below those sampled.

In the Marianas, sex ratio varied with depth for all three of the major species of *Heterocarpus*. For each species, a larger percentage of the catch is composed of females at the shallower end of the species' depth range. A similar distribution in Hawaii has been reported for *H. ensifer* (Clarke 1972) and *H. laevigatus* (Dailey and Ralston 1986).

Changes in the mean size with depth have been reported for *H. ensifer* and *H. laevigatus*. Wilder (1977) and Gooding (1984) reported increases in size with increasing depth for *H. ensifer* from Guam and the NWHI, respectively. Clarke (1972), on the other hand, found that a higher proportion of larger individuals in Hawaii occupied the depth of greatest abundance, while smaller individuals were found in shallower or deeper water. Gooding (1984) noted a

⁴Hawaiian Divers, Inc. 1983. Deepwater shrimp utilization study for Hawaii. Report prepared under NOAA Cooperative Agreement No. 80-ABH-00065 for the Southwest Region, Western Pacific Program Office, National Marine Fisheries Service, NOAA, 47 p.

decline in size (kilograms/individual) with increasing depth for *H. laevigatus* in the NWHI. In all of these studies, changes in sex ratio with depth were not taken into account. As we have shown, sex ratio does change with depth and the sexes do grow at different rates. The observed changes in size with depth may be due to changes in sex ratio rather than size-specific stratification. Dailey and Ralston (1986) examined the sexes separately and found that for *H. laevigatus* in Hawaii the carapace length of males and egg-bearing females displayed no apparent change with depth, whereas that of nonegg-bearing females showed a strong inverse relationship. In the Marianas, significant changes in mean carapace length with depth were not observed for either sex of the three species of *Heterocarpus*, except for female *H. longirostris* (Table 2). For this group, an inverse relationship was observed much like that found for nonegg-bearing female *H. laevigatus* in Hawaii (Dailey and Ralston 1986).

The estimates of growth parameters for *H. laevigatus* obtained in this study correspond well with those of other authors (Table 9). Using the regression method (Wetherall et al. in press), we estimated L_{∞} to be 51.3 mm CL for males, 55.4 mm CL for females, and 55.2 mm CL for the pooled population in the Marianas. Using the same method, Dailey and Ralston (1986) obtained estimates of 57.9 mm CL for males, 62.5 mm CL for females, and 61.7 mm CL for the combined sexes in Hawaii. Apparently, *H. laevigatus* grows about 7 mm larger in Hawaii than in the Marianas. King (1983), using the Beverton and Holt method, estimated $L_{\infty} = 57$ mm CL for *H. laevigatus* in Fiji.

Estimates of Z/K for *H. laevigatus* in the Marianas were 2.1 for males, 1.9 for females, and 2.5

for the sexes combined. In Hawaii, Z/K estimates of 4.3, 2.9, and 2.6 were obtained for the same categories, respectively (Dailey and Ralston 1986). The Z/K estimates for the combined sexes are nearly identical in the two studies. In our study, Z/K estimates for the two sexes were similar to each other and lower than that of the sexes combined, whereas in the Hawaii study they were very different from each other and both larger than that of the combined sexes. In our study, if we assume that instantaneous growth of the two sexes is similar, then mortality will also be similar and close to the 0.75 yr^{-1} value estimated for the pooled sexes. In the Hawaii study, Z/K estimates for males and females differed widely. Mortality estimates differed considerably as well, $Z = 1.51 \text{ yr}^{-1}$ for males and 0.73 yr^{-1} for females.

The K parameter for *H. laevigatus* in the Marianas was estimated as $K = 0.30 \text{ yr}^{-1}$ for the combined sexes (Table 9). Estimates of K for the individual sexes were ambiguous and inconsistent. King (1983) estimated K as 0.27 yr^{-1} for *H. laevigatus* in Fiji and Dailey and Ralston (1986) estimated K as 0.35 yr^{-1} for male and 0.25 yr^{-1} for female *H. laevigatus* in Hawaii. Because growth estimates for *H. laevigatus* are similar for the various areas studied, it is not surprising that estimates of age at maturity are also similar (Table 9). King (1983) reported the age at maturity for female *H. laevigatus* in the South Pacific as 4.6 years (40.5 mm CL). He further suggests that males mature at about 24 mm CL (age not calculated). Dailey and Ralston (1986) found that females in Hawaii mature at 40 mm or about 4 years. In the Marianas female maturity is estimated at 43 mm CL or about 4.5 years. Males mature earlier at 35.7 mm CL or about 3.0 to 3.5 years. Male maturity estimates by King (1983) and this study are based on the relative growth of the appendix masculina on the second pleopod. King appeared to have chosen 50% of the asymptotic value as the point of maturity much as the point where 50% of the female shrimp are bearing eggs is used to define maturity for females. We feel that 90% of the asymptotic value is a better estimate of male maturity and have used that point in our estimate for the Marianas.

ACKNOWLEDGMENTS

This manuscript is a result of the Resource Assessment Investigation of the Mariana Archipelago (RAIOMA) program conducted by the National Marine Fisheries Service, Southwest Fisheries Center Honolulu Laboratory. We thank the faculty, staff, and students of the University of Guam

TABLE 9.—Asymptotic length (L_{∞}), instantaneous growth constant (K), length at maturity (L_M), and age at maturity (T_M) of *Heterocarpus laevigatus*.

Location	L_{∞} (mm)	K (yr^{-1})	L_M	T_M
Fiji				
(King 1983)				
Sexes combined	57	0.27		
Females			40.5	4.6
Males			24	
Hawaii				
(Dailey and Ralston 1986)				
Sexes combined	61.7			
Females	62.5	0.25	40	4
Males	57.9	0.35		
Mariana Archipelago				
(present study)				
Sexes combined	55.2	0.30		
Females	55.4		43	4.5
Males	51.3		36	3.5

Marine Laboratory for their assistance and participation during the field period. We also thank the staffs of the Division of Aquatic and Wildlife Resources of the Territory of Guam and the Division of Fish and Wildlife of the Commonwealth of the Northern Mariana Islands for their cooperation throughout the study.

LITERATURE CITED

- BEDDINGTON, J. R., AND J. G. COOKE.
1983. The potential yield of fish stocks. FAO Fish. Tech. Pap. 242, 47 p.
- BEVERTON, R. J. H., AND S. J. HOLT.
1956. A review of methods for estimating mortality rates in fish populations, with special reference to sources of bias in catch samplings. Rapp. P.-v. Réun. CIEM, 140:67-83.
- BUTLER, T. H.
1964. Growth, reproduction and distribution of pandalid shrimps in British Columbia. J. Fish. Res. Board Can. 21: 1403-1452.
- CLARKE, T. A.
1972. Exploration for deep benthic fish and crustacean resources in Hawaii. Univ. Hawaii, Hawaii Inst. Mar. Biol., Tech. Rep. 29, 18 p.
- DAILEY, M. D., AND S. RALSTON.
1986. Aspects of the reproductive biology, spatial distribution, growth, and mortality of the deepwater caridean shrimp *Heterocarpus laevigatus* in Hawaii. Fish. Bull., U.S. 84:915-925.
- FAO.
1984. 1982 Yearbook of fishery statistics; catches and landings. FAO, Rome 54, 393 p.
- GOODING, R. M.
1984. Trapping surveys for the deepwater caridean shrimps, *Heterocarpus laevigatus* and *H. ensifer*, in the Northwestern Hawaiian Islands. Mar. Fish. Rev. 46(2):18-26.
- GULLAND, J. A.
1969. Manual of methods for fish stock assessment. Part 1. Fish population analysis. FAO Fish. Ser. 3, 154 p.
1983. Fish stock assessment. A manual of basic methods. John Wiley & Sons, N.Y., 223 p.
1984. Advice on target fishery rates. Fishbyte [ICLARM] 2(1):8-11.
- GUNDERSON, D. R., P. CALLAHAN, AND B. GOINEY.
1980. Maturation and fecundity of four species of *Sebastes*. Mar. Fish. Rev. 42(3-4):74-79.
- HOLTHUIS, L. B.
1980. Shrimps and prawns of the world. An annotated catalogue of species of interest to fisheries. FAO Fish. Synop. (125) vol. 1, 261 p.
- KARIG, D. E.
1971. Structural history of the Mariana Islands arc system. Bull. Geol. Soc. Am. 82:323-344.
- KING, M. G.
1980. A trapping survey for deepwater shrimp (Decapoda: Natantia) in Western Samoa. Rep. Inst. Mar. Res., Univ. South Pacific, Fiji, 26 p.
1981a. Deepwater shrimp resources in Vanuatu: a preliminary survey off Port Vila. Mar. Fish. Rev. 43(12):10-17.
1981b. The deepwater shrimps of Tonga: a preliminary survey near Nuku'alofa. Rep. Inst. Mar. Res. Univ. South Pacific, Fiji, 29 p.
1983. The ecology of deepwater caridean shrimps (Crustacea: Decapoda: Caridea) near tropical Pacific islands with particular emphasis on the relationship of life history patterns to depth. Ph.D. Thesis, Univ. South Pacific, Suva, Fiji, 258 p.
1984. The species and depth distribution of deepwater caridean shrimps (Decapoda, Caridea) near some southwest Pacific islands. Crustaceana 47(2):174-191.
- KING, M. G., AND R. B. MOFFITT.
1984. The sexuality of tropical deepwater shrimps (Decapoda: Pandalidae). J. Crust. Biol. 4(4):567-571.
- MOFFITT, R. B.
1983. *Heterocarpus longirostris* MacGillchrist from the Northern Mariana Islands. Fish. Bull., U.S. 81:434-436.
- OISHI, F.
1983. Pacific Tuna Development Foundation - State of Hawaii shrimp industry development project. Division of Aquatic Resources, Department of Land and Natural Resources, State of Hawaii, 22 p.
- PAULY, D.
1982. Studying single-species dynamics in a tropical multi-species context. In D. Pauly and G. I. Murphy (editors), Theory and management of tropical fisheries, p. 33-70. ICLARM and CSIRO, Manila.
- POLOVINA, J. J., R. B. MOFFITT, S. RALSTON, P. M. SHIOTA, AND H. A. WILLIAMS.
1985. Fisheries resource assessment of the Mariana Archipelago. 1982-85. Mar. Fish. Rev. 47(4):19-25.
- POLOVINA, J. J., AND S. RALSTON.
1986. An approach to yield assessment for unexploited resources with applications to the deep slope fishes of the Marianas. Fish. Bull., U.S. 84:759-770.
- RALSTON, S.
1986. An intensive fishing experiment for the caridean shrimp, *Heterocarpus laevigatus*, at Alamagan Island in the Mariana Archipelago. Fish. Bull., U.S. 84:927-934.
- STRUHSAKER, P., AND D. C. AASTED.
1974. Deepwater shrimp trapping in the Hawaiian Islands. Mar. Fish. Rev. 36(10):24-30.
- STRUHSAKER, P., AND H. O. YOSHIDA.
1975. Exploratory shrimp trawling in the Hawaiian Islands. Mar. Fish. Rev. 37(12):13-21.
- WESTERN PACIFIC REGIONAL FISHERY MANAGEMENT COUNCIL.
1984. Status of fisheries assessment of development and management needs for selected crustacean species in the Western Pacific region. Western Pacific Regional Fishery Management Council, Honolulu, HI, 60 p.
- WETHERALL, J. A., J. J. POLOVINA, AND S. RALSTON.
In press. Estimating growth and mortality in steady state fish stocks from length-frequency data. In D. Pauly and G. R. Morgan (editors), Length-based methods in fishery research. ICLARM Conf. Proc. Manila, vol. 1.
- WILDER, M. J.
1977. Biological aspects and fisheries potential of two deepwater shrimps *Heterocarpus ensifer* and *Heterocarpus laevigatus* in waters surrounding Guam. M.S. Thesis, Univ. Guam, Agaña, 79 p.

ESTIMATION OF AGE AND GROWTH RATE IN NORWEGIAN SPRING SPAWNING HERRING (*CLUPEA HARENGUS* L.) LARVAE AND JUVENILES

ERLEND MOKSNESS, JOHN BUTLER & RICHARD L. RADTKE

SARSIA



MOKSNESS, ERLEND, JOHN BUTLER & RICHARD L. RADTKE 1987 12 15. Estimation of age and growth rate in Norwegian spring spawning herring (*Clupea harengus*) larvae and juveniles. – *Sarsia* 72:341–342. Bergen. ISSN 0036–4827.

Herring larvae and juveniles were aged by use of developmental stages and daily growth increments in the otoliths. The results indicate that developmental stages are useful in ageing larvae till the end of the yolk-sac stages, while daily growth increments in the otoliths are to be preferred in older larvae and juveniles.

Erlend Moksness, Flødevigen Biological Station, N-4800 Arendal, Norway. – John Butler, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038, USA. – Richard L. Radtke, University of Hawaii at Manoa, P.O. Box 1346, Coconui Island, Kaneohe, HI 96744, USA.

The age and growth rate of larvae and juveniles of the Norwegian spring spawning herring (*Clupea harengus* L.) taken in the field bring about considerable indefiniteness. The purpose of the present study was to test existing methods for estimation of age and back-calculation of growth rate.

The herring were stripped at the spawning area in western Norway and the fertilized eggs were incubated in the laboratory at Flødevigen Biological Station. Newly hatched herring larvae were transferred to starving and feeding experiments at four temperatures, 3.5, 5.0, 6.5, and 8.0° C in the laboratory and one group was released in a 2500 m³ outdoor basin. The herring larvae used were from different hatching dates, however, larvae in each experiment were hatched within 24 hours. Daily samples in the laboratory were both frozen and preserved in formaldehyde. Those preserved in formaldehyde were later examined for standard length, dry weight, yolk-sac volume, gut content, and developmental stages according to DOYLE (1977) and ØIESTAD (1983). The sagittae in the frozen larvae from the laboratory experiments and in the frozen juveniles from the basin experiment were dissected out and mounted on a glass slide. Standard length and dry weight of the fishes were measured. A few otoliths were later examined in a Scanning Electron Microscope (SEM) and 100 otolith pairs were examined using an otolith reading system, developed at SWFC, La Jolla (METHOT & KRAMER 1979). The otolith reading system consisted of a video camera attached to a light microscope with a magnification up to 1000 times, a monitor, a digitizer, and a micro-computer. The otoliths were read in several subsessions as the rings were exposed by grinding. The micro-computer received data on the number of rings and the distances between the

observed rings. Two software programmes were used to estimate the age and back-calculate the growth rate of each larva or juvenile. The radius of the nucleus and the initial distances between the rings in the otoliths were measured to respectively 10 µm and 0.6–0.8 µm by the help of SEM.

The estimated age of the laboratory-reared larvae was from 20 to 30 days less than their real age. The cause of the difference is probably the low growth rate (less than 0.10 mm/day) observed on the laboratory groups from the end of yolk-sac stages till an age of 20 to 30 days. The estimated ages of the basin-reared herring juveniles were all from 9 to 11 days less than their real age. This corresponds with earlier observations on herring larvae where they start laying down daily rings from the end of yolk-sac stages (LOUGH & al. 1982, MCGURK 1984). The back-calculated growth rate of the basin-reared herring corresponds with earlier observations on the growth rate of basin-reared larvae (GJØSÆTER & ØIESTAD 1981). Table 1 gives the main results from the staging of the herring larvae. The results accord with the observations by DOYLE (1977). The yolk-sac herring larvae can be aged within three to eight days of their actual age. The duration of later stages are more than 10 days, which is a too big error for age estimation.

Table 1. The duration of the different sub-developmental stages of fed herring larvae (*Clupea harengus* L.) at 6.5° C in the laboratory. Stages according to DOYLE (1977) and ØIESTAD (1983).

Stages	1a	1b	1c	1d	2a
Present study	3.6	3.2	6.1	6.5	–
DOYLE (1977)	3.2	3.7	3.9	–	16.6

In conclusion stageing herring larvae according to DOYLE (1977) and ØIESTAD (1983) could be useful for estimating the age in yolk-sac herring larvae, while larvae that have passed the yolk-sac stage should be aged by their otoliths. The latter method will in addition give the growth rate of the larvae from the end of the yolk-sac stage.

REFERENCES

- Doyle, M.J. 1977. A morphological staging system for the larval morphology of the herring, *Clupea harengus* L. – *Journal of the Marine Biological Association of the United Kingdom* 57:859–867.
- Gjøsæter, H. & V. Øiestad 1981. Growth pattern in otoliths as an indication of daily growth variation of larval herring (*Clupea harengus*) from experimental ecosystem. – *International Council for the Exploration of the Sea* H31:1–7 (mimeo).
- Lough, R.G., M. Pennington, G.R. Bolz & A.A. Rosenberg 1982. Age and growth of Atlantic herring, *Clupea harengus* L., in the Gulf of Maine-Georges Bank region based on otolith growth increments. – *Fishery Bulletin US* 80:187–199.
- McGurk, M.D. 1984. Ring deposition in the otoliths of larval pacific herring, *Clupea harengus pallasii*. – *Fishery Bulletin US* 82:113–120.
- Methot, R.D.Jr. & D. Kramer 1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. *Fishery Bulletin US* 72:413–423.
- Øiestad, V. 1983. *Growth and survival of herring larvae and fry (Clupea harengus L.) exposed to different feeding regimes in experimental ecosystems: outdoor basin and plastic bags.* – Dr.philos. thesis, University of Bergen, 299 pp.

Accepted 20 May 1987.

L-(+)-Lactate translocation into the red blood cells of the skipjack tuna (*Katsuwonus pelamis*)

T. W. MOON,¹ R. W. BRILL, P. W. HOCHACHKA,² AND J.-M. WEBER²

Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, National Oceanographic and Atmospheric Administration, Honolulu, HI, U.S.A. 96812

Received November 28, 1986

MOON, T. W., BRILL, R. W., HOCHACHKA, P. W., and WEBER, J.-M. 1987. L-(+)-Lactate translocation into the red blood cells of the skipjack tuna (*Katsuwonus pelamis*). *Can. J. Zool.* **65**: 2570–2573.

Red blood cells from skipjack tuna, *Katsuwonus pelamis*, were incubated *in vitro* in various concentrations of L-(+)-lactate. There was no significant effect of pH between 6.6 and 8.1 on inward lactate translocation. Because there was a linear response between translocation rate and lactate added (up to 30 mM), we propose that a diffusive mechanism is the primary mode of lactate translocation into tuna red blood cells at least over the range of concentrations tested. This mechanism is unlike that reported for lactate influx in other animal cell types and may result from the reported differences in the control of proton movements across the red blood cell membrane of fish species.

MOON, T. W., BRILL, R. W., HOCHACHKA, P. W., et WEBER, J.-M. 1987. L-(+)-Lactate translocation into the red blood cells of the skipjack tuna (*Katsuwonus pelamis*). *Can. J. Zool.* **65**: 2570–2573.

Des hématies de la Thonine à ventre rayé, *Katsuwonus pelamis*, ont été gardées *in vitro* à diverses concentrations de L-(+)-lactate. Le pH, dans l'intervalle 6,6 à 8,1, reste sans effet sur la translocation vers l'intérieur du lactate. Puisqu'il y a une relation linéaire entre le taux de translocation et la quantité de lactate ajoutée (jusqu'à 30 mM), il est probable qu'un mécanisme de diffusion soit le principal mode de translocation du lactate dans les hématies de la thonine, au moins dans les conditions de l'expérience. Ce mécanisme diffère de celui qui est évoqué pour expliquer l'influx de lactate dans d'autres cellules animales, peut-être à cause des différences observées dans le contrôle des mouvements de protons à travers les membranes des hématies de poissons.

[Traduit par la revue]

Introduction

Lactate translocation across membranes of mammalian cell types, including human red blood cells (Dubinsky and Racker

1978), hepatocytes (Monson et al. 1981; Fafournoux et al. 1985), and tumor cells (Spencer and Lehninger 1976; Johnson et al. 1980), is dependent upon extracellular pH (pH_e) and involves a specific monocarboxylate transporter coupled to either a H^+ -symport or an OH^- -antiport. Cell types of other vertebrates, including fish, have not been investigated in this regard.

This study examines lactate translocation across the red blood cell membrane of the skipjack tuna, *Katsuwonus pelamis*. This species can produce high white muscle lactate concentrations

¹Department of Biology, University of Ottawa, Ottawa, Ont., Canada K1N 6N5 (address for correspondence and reprint requests) and Huntsman Marine Laboratory, St. Andrews, N.B., Canada E0G 2X0.

²Permanent address: Department of Zoology, University of British Columbia, Vancouver, B.C., Canada V6T 2A9.

during burst activity (Guppy et al. 1979), with peak circulating lactate levels exceeding 25 mM (Guppy et al. 1979; Perry et al. 1985), and displays lactate disappearance rates comparable to those of mammals (Weber et al. 1986). Perry et al. (1985) reported that blood pH drops by approximately 0.5 pH units during exhausting exercise, but that both protons and lactate are rapidly removed from the blood (less than 50 min). These significant fluctuations in plasma pH and lactate concentrations make this species ideally suited for investigations of lactate translocation into red blood cells.

Materials and methods

Skipjack tuna, *Katsuwonus pelamis*, were captured on hook and line by local fishermen, transported to the Kewalo Research Facility, and held in large circular outdoor tanks supplied with rapidly flowing seawater at 25°C. The fish were not fed and were used within the first 4 days of capture. Each fish (weight, 1.5–3.0 kg) was netted and stunned by a blow to the head, the heart was exposed, and blood was collected into heparinized syringes (syringes were rinsed with 5000 U sodium heparin/mL) from the exposed heart; this procedure took less than 2 min. The blood was centrifuged (Sorvall SS-1 Superspeed; approximately 1500 rpm) at 18°C and the red blood cells were gently resuspended and washed two times with cold 0.15 M NaCl according to Kim and Isaacs (1978). The buffy layer was carefully removed during this procedure. Little or no hemolysis was noted during these procedures. Experiments were performed with the blood of individuals; pooling was not necessary.

Lactate flux measurements were carried out according to Kim and Isaacs (1978). The red blood cells were resuspended in a modified teleost Ringer's solution (150 mM NaCl, 2.4 mM KCl, 5 mM NaHCO₃, 2 mM MgCl₂, 2.6 mM NaH₂PO₄, 1.4 mM CaCl₂, pH adjusted to 6.6, 7.6, or 8.1) and the pH was checked with a standard electrode; any adjustments were made by adding weak acid or base to the suspension. The hematocrit was adjusted to approximately 10%, or about 25% of normal (Perry et al. 1985; this study, data not reported). The final hematocrit was estimated by weighing 1 mL of resuspension, centrifuging for 5 min (Eppendorf model 3200 microcentrifuge; Brinkmann Instruments), removing the plasma including the adhering fluids, and reweighing the pellet.

Incubations were carried out at 20°C in 50-mL Erlenmeyer flasks, open to the atmosphere, which were frequently shaken. L-(+)-Lactate was added as the sodium salt and [¹⁴C(U)]lactate (New England Nuclear, Boston; specific activity 109 mCi·mmol⁻¹; 1 mCi = 37 kBq) was added to obtain a final activity of 0.2 µCi·mL⁻¹ of medium; the specific activity of the incubation medium was based on the measured lactate concentration and the counts in an aliquot of the medium at time zero. All experiments were completed within 3 h of removing the red blood cells from the animal.

A 0.4-mL aliquot of the cell suspension was layered onto 0.8 mL of dibutylphthalate and immediately centrifuged (Eppendorf microcentrifuge) for 1.5 min. The upper layer along with a small amount of the oil was removed with a pasteur pipet; the tube and oil surface were rinsed twice with approximately 0.75 mL of distilled water before the remaining oil was carefully removed. The tube walls were wiped dry with a Kimwipe. The red blood cells were deproteinized by adding 0.4 mL of 8% perchloric acid, mixing with a vortex, and allowing the suspension to sit for 30 min on ice before centrifuging as above. An aliquot of the clear, acidified supernatant was added to scintillation fluid (ACS II, Amersham Corporation, IL) and counted for radioactivity (Beckman scintillation counter model 3600 with internal standard quench correction). Trapped extracellular volume was not estimated, but is reported to be less than 5% using similar procedures (Kim and Isaacs 1978; Houston and Tun 1986; T. W. Moon, unpublished data). Transport rates were estimated from the specific activity of the medium at time zero and the radioactivity in the cell pellet, and related to the mass of red blood cells as calculated from the final hematocrit value.

L-(+)-Lactate concentrations of the standard solutions were estimated enzymatically (Bergmeyer 1974).

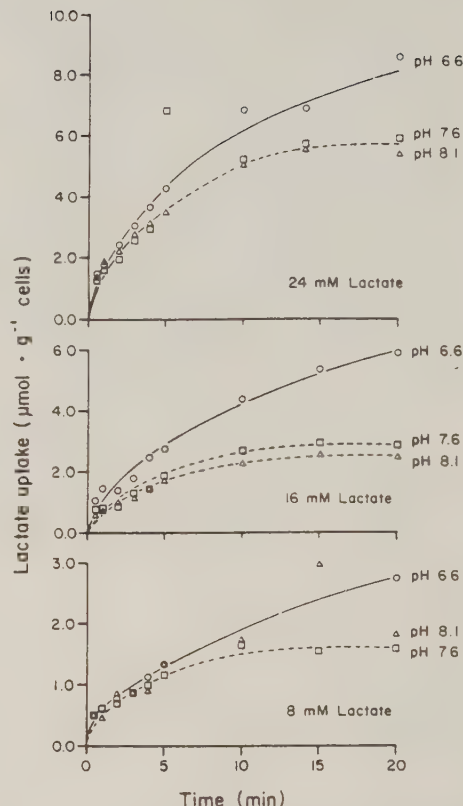


FIG. 1. Time course of lactate uptake and accumulation into skipjack tuna red blood cells as a function of pH and lactate concentration. Incubations were at 20°C and a hematocrit of approximately 10%. Each point represents a single sample.

Results

Lactate translocation into washed, resuspended skipjack red blood cells was curvilinear with time (Fig. 1), as it is in mammalian cells (Spencer and Lehninger 1976; Fafourmoux et al. 1985). There were no differences in initial rates of translocation when the medium or extracellular pH (pH_e) was decreased from 8.1 to 7.6; a steady state was observed within 10 min at these pHs. A general trend for rates to increase at pH 6.6 occurred after the initial 10-min incubation time; this was a function of substrate concentration. These differential pH effects with time suggest that uptake rates do not follow simple saturation isotherms.

Initial rates of lactate translocation are a linear function of external lactate concentrations between 1 and 30 mM, and independent of extracellular pH between 6.6 and 8.1 in skipjack red blood cells (Fig. 2). The curvilinear uptake rates shown in Fig. 1 made the selection of a time for kinetic studies difficult and somewhat arbitrary as reported in other slowly transporting lactate systems (Spencer and Lehninger 1976). A 3-min period was selected (Fig. 2), as initial rates were of interest for comparison with mammalian studies. If 20 min had been selected, rates at pH 6.6 would have been higher, but not significantly so when compared with pH 7.6 or 8.1, nor would the shape of the kinetic response have been altered. These data

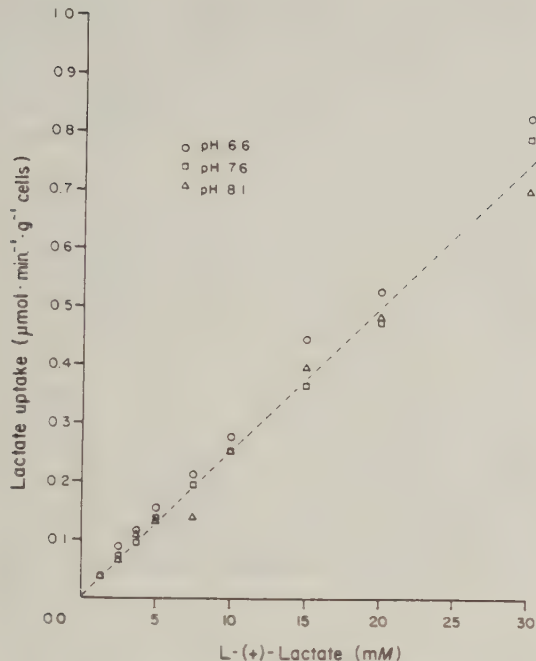


FIG. 2. Kinetics of lactate uptake into skipjack tuna red blood cells. Cells (approx. 10% hematocrit) were incubated for 3 min at 20°C at the appropriate concentration of L-(+)-lactate before being separated through oil (see Materials and methods). Each value represents the mean of two separate experiments.

suggest a prime diffusive component for lactate uptake in tuna red blood cells unlike the situation in mammalian cells.

Discussion

The interpretation of these tuna red blood cell data is made difficult by the lack of studies reported in this area. In addition, many factors affect the composition of teleost red blood cells in suspension (see Houston and Tun 1986; Nikinmaa 1986). The methods used here, however, are consistent with those of other studies in the literature, and should not affect the transport characteristics of these cells. Measurements of intracellular pH would have aided the interpretation of the data, but unfortunately we did not have access to the appropriate equipment for such an analysis.

The absence of a significant pH_e effect on the translocation rate, except possibly at very low pH_e s, and a linear response between the translocation rate and lactate concentration suggest significant differences in these processes between the skipjack tuna red blood cell and the mammalian cell systems studied to date. A sharp increase in translocation rates at all time intervals and substrate concentrations with pH decreases have been reported in mammalian cells at pH_e s between about 8.0 and 6.0 (Spencer and Lehninger 1976; Dubinsky and Racker 1978; Fafournoux et al. 1985). This result supports the role of the transmembrane pH or proton gradient in the lactate uptake mechanism (Spencer and Lehninger 1976; Dubinsky and Racker 1978). Although a diffusive translocation component may exist *in vivo* in mammalian cells, its contribution to lactate influx is thought to be small at physiological lactate concentrations of 1–5 mM (Spencer and Lehninger 1976; Fafournoux et

al. 1985). Lactate translocation in these mammalian cell systems occurs primarily by a monocarboxylate transporter which is coupled to proton movements and thus is strongly pH dependent. Thus, differences between the tuna and mammalian systems may involve the distribution of protons across the cell membrane and the regulation of intracellular pH (pH_i), although other possibilities cannot be excluded.

It is generally accepted that protons are passively distributed across the non-nucleated mammalian red blood cell according to a simple Donnan equilibrium. This is due to the high efficiency of the anion transport system of the band 3 protein, and is unique to the red blood cell (Roos and Boron 1981; Borgese et al. 1986). With few exceptions (see Hemming et al. 1986), a similar situation is thought to occur in the fish red blood cell. However, differences have been reported in the response of pH_i to changes in pH_e between these red blood cell types. The slope of the pH_i – pH_e relationship for the mammalian red blood cell is -0.37 (Freedman and Hoffman 1979; Zock et al. 1980), while the value for rainbow trout red blood cells varies between -0.47 (Hemming et al. 1986) and -0.90 (Perry and Vermette 1987) with a value of about -0.70 the most frequently reported (Albers and Goetz 1985; C. L. Milligan and C. M. Wood, personal communication). The consequence of these different slope values is that the proton gradient across the mammalian red blood cell will be greater at low pH_e than that of the fish cell. A reduction in pH_e stimulates lactate uptake into mammalian red blood cells (Dubinsky and Racker 1978), probably through this increase in the magnitude of the proton gradient across the cell membrane. The minor pH_e effect on lactate translocation in tuna red blood cells reported here (Figs. 1 and 2) could be explained if the pH_i – pH_e relationship for tuna is in the range reported by Perry and Vermette (1987) for trout.

Active fish species, such as the trout and the tuna, show significant decreases in pH_e after exhaustive exercise (Wood and Perry 1985). This plasma acidification results in minor changes in pH_i (Nikinmaa et al. 1984; Primmitt et al. 1986; C. L. Milligan and C. M. Wood, personal communication). Epinephrine and norepinephrine released into the circulation during exercise are thought to accomplish this regulatory response by activating the red blood cell sodium–proton antiport mechanism leading to cell alkalization and the maintenance of hemoglobin–oxygen binding capacity (Baroin et al. 1984; Nikinmaa 1986). This *in vivo* response can be duplicated in rainbow trout red blood cells *in vitro* by adding epinephrine to the suspension (Nikinmaa 1986; Perry and Vermette 1987). Should epinephrine *in vivo* or *in vitro* lead to similar changes in tuna red blood cells, proton gradients across the membrane would increase. In this way, the tuna red blood cell may more closely resemble the mammal cell, with lactate translocation correlated with the extent of the proton gradient.

These experiments suggest that a major difference exists between the *in vitro* translocation of lactate across the red blood cell membrane of mammals and tuna. The precise explanation for this difference is not known, although epinephrine sensitivity may be important. Further studies are necessary to evaluate these transport differences, especially with respect to known inhibitors of anion and cation transport systems and catecholamines. A recent study (P. J. Walsh, personal communication) has found that lactate translocation into isolated rainbow trout hepatocytes is also a diffusion-limited process and quite unlike that reported in mammalian hepatocytes.

Acknowledgements

This study was funded by National Marine Fisheries Service

- and by operating grants from the Natural Sciences and Engineering Research Council of Canada to T.W.M. and P.W.H. As visitors to the Kewalo Research Facility, T.W.M., P.W.H., and J.-M.W. wish to thank the entire staff for their cooperation and hospitality during this study. Special thanks are extended to Drs. G. Ahearn and F. Kamamoto, Department of Zoology, and Dr. X. Karl, Department of Oceanography, University of Hawaii, for the use of equipment essential to the completion of this study. T.W.M. would like to thank Dr. S. F. Perry, Department of Biology, University of Ottawa, for his scintillating discussion which assisted in formulating the Discussion section.
- ALBERS, C., and GOETZ, K. G. 1985. H^+ and Cl^- ion equilibrium across the red cell membrane in the carp. *Respir. Physiol.* **61**: 209–219.
- BAROIN, A., GARCIA-ROMEU, F., LAMARRE, T., and MOTAIS, R. 1984. Hormone-induced co-transport with specific pharmacological properties in erythrocytes of rainbow trout, *Salmo gairdneri*. *J. Physiol.* **350**: 137–157.
- BERGMEYER, H.-U. 1974. *Methods of enzymatic analysis*. 2nd ed. Academic Press, New York.
- BORGES, F., GARCIA-ROMEU, F., and MOTAIS, R. 1986. Catecholamine-induced transport systems in trout erythrocyte. Na^+/H^+ countertransport or $NaCl$ cotransport? *J. Gen. Physiol.* **87**: 551–566.
- DUBINSKY, W. P., and RACKER, E. 1978. The mechanism of lactate transport in human erythrocytes. *J. Membr. Biol.* **44**: 25–36.
- FAFOURNOUX, P., DEMIGNE, C., and REMESY, C. 1985. Carrier-mediated uptake of lactate in rat hepatocytes. Effects of pH and possible mechanisms for L-lactate transport. *J. Biol. Chem.* **260**: 292–299.
- FREEDMAN, J. C., and HOFFMAN, J. F. 1979. Ionic and osmotic equilibria of human red blood cells treated with nystatin. *J. Gen. Physiol.* **74**: 157–185.
- GUPPY, M., HULBERT, W. C., and HOCHACHKA, P. W. 1979. Metabolic sources of heat and power in tuna muscles. II. Enzyme and metabolite profiles. *J. Exp. Biol.* **82**: 303–320.
- HEMMING, T. A., RANDALL, D. J., BOUTILIER, R. G., IWAMA, G. K., and PRIMMETT, D. 1986. Ionic equilibrium in red blood cells of rainbow trout (*Salmo gairdneri*): Cl^- , HCO_3^- , and H^+ . *Respir. Physiol.* **65**: 223–234.
- HOUSTON, A. H., and TUN, N. 1986. Environmentally-related changes in red cell levels of ionic modulators of hemoglobin- O_2 affinity in rainbow trout, *Salmo gairdneri*. *Comp. Biochem. Physiol.* **A, 85**: 779–783.
- JOHNSON, J. H., BELT, J. A., DUBINSKY, W. P., ZIMNIAK, A., and RACKER, E. 1980. Inhibition of lactate transport in Ehrlich ascites tumor cells and human erythrocytes by a synthetic anhydride of lactic acid. *Biochemistry*, **19**: 3836–3840.
- KIM, H. D., and ISAACKS, R. E. 1978. The membrane permeability of nonelectrolytes and carbohydrate metabolism of Amazon fish red cells. *Can. J. Zool.* **56**: 863–869.
- MONSON, J. P., SMITH, J. A., COHEN, R. D., and ILES, R. A. 1981. Characterization of the hepatocyte plasma membrane transport mechanism for lactate. *Clin. Sci.* **60**: 4P–5P.
- NIKINMAA, M. 1986. Control of red cell pH in teleost fishes. *Ann. Zool. Fenn.* **23**: 223–235.
- NIKINMAA, M., CECCH, J. J., and MCENROE, M. 1984. Blood oxygen transport in stressed striped bass (*Morone saxatilis*); role of beta-adrenergic responses. *J. Comp. Physiol.* **154**: 365–369.
- PERRY, S. F., and VERMETTE, M. G. 1987. The effects of prolonged epinephrine infusion on the physiology of the rainbow trout, *Salmo gairdneri*. I. Blood respiratory, acid–base and ionic states. *J. Exp. Biol.* **128**: 235–253.
- PERRY, S. F., DAXBOECK, C., EMMETT, B., HOCHACHKA, P. W., and BRILL, R. W. 1985. Effects of exhausting exercise on acid–base regulation in skipjack tuna (*Katsuwonus pelamis*) blood. *Physiol. Zool.* **58**: 421–429.
- PRIMMETT, D. R. N., RANDALL, D. J., MAZEUD, M., and BOUTILIER, R. G. 1986. The role of catecholamines in erythrocyte pH regulation and oxygen transport in rainbow trout (*Salmo gairdneri*) during exercise. *J. Exp. Biol.* **122**: 139–148.
- ROOS, A., and BORON, W. F. 1981. Intracellular pH. *Physiol. Rev.* **61**: 296–434.
- SPENCER, T. L., and LEHNINGER, A. L. 1976. L-Lactate transport in Ehrlich ascites tumour cells. *Biochem. J.* **154**: 405–414.
- WEBER, J.-M., BRILL, R. W., and HOCHACHKA, P. W. 1986. Mammalian metabolite flux rates in a teleost: lactate and glucose turnover in tuna. *Am. J. Physiol.* **250**: R452–R458.
- WOOD, C. M., and PERRY, S. F. 1985. Respiratory, circulatory, and metabolic adjustments to exercise in fish. *In* *Circulation, respiration, and metabolism*. Edited by R. Gilles. Springer-Verlag, Berlin. pp. 2–22.
- ZOCK, J. P., RISPENS, P., and ZIJLSTRA, W. G. 1980. Carbon dioxide loading and the acid–base equilibrium states of human blood. *Proc. K. Ned. Akad. Wet. Ser. C*. **83**: 307–332.

Descriptions of Reared Larvae of Six Species of *Sebastes*

H. GEOFFREY MOSER

JOHN L. BUTLER

Southwest Fisheries Center

National Marine Fisheries Service, NOAA

La Jolla, CA 92038

ABSTRACT

This paper describes techniques used in rearing larvae obtained from field-caught females of six species of rockfishes (*Sebastes*). The early larval stages are described for three of these species (*S. entomelas*, *S. serranoides*, and *S. rubrivinctus*) and more complete larval series are described for three other species (*S. rufus*, *S. ovalis*, and *S. constellatus*). The larval taxonomic characters of these species are compared with those of other rockfish species. Experiments on yolk-sac larvae of *S. rubrivinctus* showed that sinking rates decrease with decreasing yolk volume and point to the precise timing of ontogeny and birth in *Sebastes*.

INTRODUCTION

Estimation of spawning biomass by sampling eggs and larvae has been accomplished for important fish stocks off California (Ahlstrom 1954, 1966, 1968; Smith 1972). Rockfishes are highly fecund live-bearers whose newborn young are at a developmental stage similar to the first-feeding larvae of typical pelagic spawners (Moser 1967). Since their larvae are abundant and widespread over the CalCOFI (Calif. Coop. Oceanic Fish. Invest.) sampling area (Ahlstrom 1961; Ahlstrom et al. 1978), there is a potential for spawning biomass estimation from ichthyoplankton samples. This potential is confounded by the large number of species (62 off California; Hubbs et al. 1979) and the relative paucity of larval characters.

Identification of larvae of eastern Pacific rockfishes has proceeded slowly. Complete developmental series, from newborn individuals to the juvenile stage, are known for eight species: *S. aurora*, *S. cortezi*, *S. dallii*, *S. jordani*, *S. levis*, *S. macdonaldi*, *S. melanostomus*, and *S. paucispinis* (Moser et al. 1977; Moser and Ahlstrom 1978; Moser et al. 1985). These identifications have been accomplished by comparing the full-term larvae from identified females with the smallest larvae of distinct series obtained from plankton hauls. Also, newly transformed identifiable juveniles with remnants of larval pigmentation and morphological features were used, along with meristic characters, to identify larval series. Using the latter technique, Richardson and Laroche (1979) and Laroche and Richardson (1980, 1981) have described postflexion larvae and early juveniles of the widow rockfish (*S. entomelas*) and nine other species. This opens the possibility for estimation of recruitment, providing these stages can be sampled adequately. Our plankton samples are dominated by early larval stages (Fig. 1) and may allow estimation of spawning biomass when critical information on fecundity, mortality, and duration of the early pelagic phase becomes available.

Progress in the identification of rockfish larvae is dependent on rearing developmental species. Although Japanese workers have been successful in rearing *Sebastes* larvae (Table 1), the rearing of an eastern Pacific species to the juvenile stage has been accomplished only recently (Moser and Butler 1981). More recently Stahl-Johnson 1985) has reared the larvae of *S. caurinus* and *S. auriculatus*

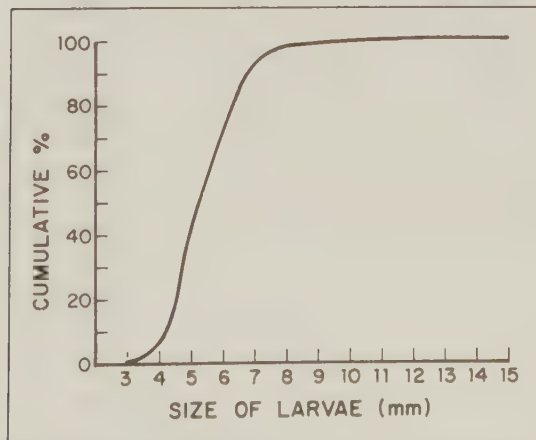


Figure 1.—Size composition of rockfish larvae in CalCOFI samples expressed in cumulative percent ($N = 11,633$).

Table 1—Summary of *Sebastes* rearing experiments.

Authors	Fujita	Fujita	Siokawa and Tsukahara	Tsukahara	Kusakari et al.	Moser and Butler
Date	1957	1958	1961	1962	1977	1981
Species	<i>S. pachycephalus</i>	<i>S. oblongus</i>	<i>S. pachycephalus</i>	<i>S. marmoratus</i>	<i>S. schlegelii</i>	<i>S. dallii</i>
Gestation period (days)	23	—	20	—	—	—
Rearing duration (days)	28	30	25	10	83	60
Food	<i>Artemia</i> nauplii	<i>Artemia</i> nauplii	<i>Artemia</i> nauplii	<i>Artemia</i> nauplii	<i>Brachionus</i> <i>Artemia</i> <i>Tigropus</i>	Wild plankton
Feeding	yes	yes	yes	no	yes	yes
Source of larvae	Female spawned in aquarium	Female spawned in aquarium	Female spawned in aquarium	Female spawned in aquarium	Female spawned in aquarium	Female spawned in field
Initial size (mm)	6.9-7.0	7.25-7.50	6-7	3.5-4.5	5.3-7.9	5.4
Final size (mm)	9.75	14	13	5	50	24.3

Table 2—Dates and locality of capture and rearing information for *Sebastes* species.

Species	Date	Locality	Method of capture	Rearing temperature (°C)	Days reared	Diet
<i>constellatus</i>	4/16/78	60 Mile Bank	Hook-and-line	14.5-16.5	38	Wild plankton
<i>entomelas</i> ¹	3/06/81	Nelson Island Oregon	Midwater trawl	10	26	<i>Brachionus</i> , wild plankton
<i>ovalis</i>	1/27/78	60 Mile Bank	Hook-and-line	13.4-16.1	29	<i>Brachionus</i> and <i>Artemia</i> nauplii to day 13; wild plankton days 13-29
<i>rubrivinctus</i>	9/15/76	Tanner Bank	Bottom trawl	9.2-14.7	Cultured for 14 days	Not fed
<i>rufus</i>	2/01/78	60 Mile Bank	Hook-and-line	13.8-16.1	46	<i>Brachionus</i> and <i>Artemia</i> nauplii to day 5; <i>Tisbe</i> nauplii days 6-8; wild plankton days 8-46
<i>rufus</i>	1/20/79	60 Mile Bank	Hook-and-line	15.6-16.0	12	Wild plankton
<i>serranoides</i>	1/18/79	Tanner Bank	Hook-and-line	16.2-17.0	16	Wild plankton

¹Information from G. W. Boehlert, Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, pers. commun.

through caudal fin formation, and G. W. Boehlert (NMFS Honolulu Lab., pers. comm.) has reared a partial series of *S. melanops*. This paper describes reared early larval stages of widow rockfish (*S. entomelas*), flag rockfish (*S. rubrivinctus*), and olive rockfish (*S. serranoides*) and more complete reared series of bank rockfish (*S. rufus*), speckled rockfish (*S. ovalis*), and starry rockfish (*S. constellatus*). Rearing was carried out at the Southwest Fisheries Center, La Jolla, California, except for the brood of *S. entomelas*, which was reared by G. W. Boehlert at the Marine Science Center, Newport, Oregon.

METHODS AND MATERIALS

Intraovarian rockfish larvae were obtained at sea by collecting near-term females with hook-and-line or by bottom trawling (Table 2). Rockfishes brought from depth often have expanded gas bladders which exert pressure on other internal organs and cause pregnant females to extrude their brood. Larvae from near-term females were collected in containers of seawater and brought back to the laboratory within one or two days for rearing. Free-swimming larvae were separated from dead ones and from those which were unable to swim off the bottom of the transport container and introduced into 100-L round black fiberglass rearing containers filled with filtered sea-

water. The containers were immersed in a water bath which maintained temperatures; an airstone was used to reduce stratification.

Larvae were fed cultured rotifers (*Brachionus plicatilis*), copepods (*Tisbe* sp.), wild plankton, or a combination of these (Table 2). Wild plankton was obtained by towing a 70- μ m mesh net in Mission Bay, San Diego, Calif. The plankton was passed through a series of screens, and the 104-254 μ m fraction, dominated by copepod nauplii, was used as food. Plankton densities in the rearing containers were maintained at 2-4 nauplii/mL, and a liter of dense algal culture, *Tetraselmis suecica* or *Dunaliella* sp., was added daily as food for the plankton.

Larvae were removed from the culture tank and preserved in 3% buffered formalin to establish life history series for analysis of morphology and pigmentation. Terminology and methods of description follow those of Moser et al. (1977) and Moser and Ahlstrom (1978).

RESULTS AND DESCRIPTIONS

Sebastes entomelas

Rearing—According to G. W. Boehlert (NMFS Honolulu Lab., pers. comm.), extruded larvae were obtained on 6 March 1981 from females collected on the FV *Centurion* at Nelson Island, Oregon. Larvae were immediately placed in jars and buckets of filtered seawater and transported to the laboratory. Those swimming were pipetted into circular black plastic pots (10-L capacity) of UV-filtered seawater with salinity $>30\text{‰}$; all larvae were held in a constant temperature room at 10°C . Within 24 hours, moribund larvae were siphoned from remaining jars and buckets and swimming larvae were transferred into a dark green circular tank (120-L capacity). After three to five days in the laboratory, rotifers were introduced at densities from 2 to 4/mL along with a dense algal culture. Subject to availability, wild zooplankton was added to the rearing tanks. Mortality was minimal to day 11, increased rapidly from day 12 to 15, with 25% of the larvae surviving on day 13, and only one larva was left on day 26.

Morphology—Six preserved samples, from day 1 to day 10, were provided by G. W. Boehlert. Extruded larvae were 4.5–4.6 mm long; a yolk sac (0.55–0.60 mm in length) and oil globule were present. Prey items were present in the stomachs of specimens preserved on day 4, even though considerable yolk remained. The yolk sac and oil globule were absent in larvae sampled after day 7. Larvae did not show appreciable growth during the 10-day period (Table 3) and reached a state of development typical of full-term broods (Fig. 2).

Pigmentation—Larvae at day 10 had melanophores along the dorsal region of the gut, below the posterior gut region, and a series on the ventral midline of the tail. The tail series extended from the third or fourth postanal myomere to the 17th–19th postanal myomere, and contained 13–16 melanophores ($\bar{x} = 14.0 \pm 0.94$ SD for 10 larvae counted). Pigment was present on the lower jaw in all specimens and melanophores were present on the brain, typically on each side of the cerebellum and optic lobes. A few specimens had 1–2 melanophores on the nape and scattered melanophores on the pectoral fin blade.

Sebastes rufus

Rearing—Larvae collected on 1 Feb. 1978 were 4.6–4.8 mm in length when stocked. The oil globule and a small yolk remnant were invested in the liver tissue. The yolk was utilized within four days; however, the oil globule persisted to the end of the first week. Larvae did not feed on *Brachionus* or *Artemia* nauplii provided through

day 5. They began feeding when nauplii and copepodites of a laboratory culture of *Tisbe* were added to the tank on day 6. Within a day the *Tisbe* moved to the sides and bottom of the container and were unavailable to the larva. Beginning on day 8, wild plankton was provided and elicited feeding activity immediately. Larvae survived until day 46.

Larvae collected on 20 Jan. 1979 were 4.3–4.7 mm in length and had a conspicuous yolk mass about 0.6 mm in diameter. They began feeding on wild copepod nauplii added that day even though the yolk mass was about 0.5 mm in diameter and occupied the anterior half of the gut region. By day 5, the yolk mass and oil globule were confined to the liver tissue. Yolk utilization was complete by the end of one week; however, the oil globule persisted one or two days more. Larvae survived until day 12.

Morphology—Larvae of *S. rufus* lack distinctive morphological features (Tables 4, 5; Fig. 2). The 6.1-mm specimen (Fig. 2D) had developing caudal rays and hypural elements and a straight notochord; the largest specimen (7.6 mm) had a completely flexed notochord (Fig. 2E). The supporting elements of the dorsal and anal fins were forming in the 7.6-mm specimen. Head spine development is similar to that observed in other species (Moser and Ahlstrom 1978). At about 6.0 mm, the following spines were forming: third posterior preopercular, second and fourth anterior preopercular, pterotic, and parietal. In the 7.6-mm specimen, the second and fourth posterior preopercular spines were also present. The postocular spine was just beginning to form above the eye. The parietal spines were relatively short and flat against the head.

Pigmentation—Newborn larvae had one or two melanophores above the brain, one at the nape, a dorsal melanistic shield above the gut, and a short postanal series along the ventral midline (Fig. 2). The ventral midline series extended from the fifth and sixth postanal myomere to the 14th–18th postanal myomere and contained 8–13 melanophores ($\bar{x} = 10.3 \pm 1.54$ SD for all specimens in growth series). Dorsal midline melanophores appeared soon after extrusion and increased in number in two stanzas up to the notochord flexion stage ($\bar{x} = 2.0 \pm 1.24$ SD for specimens in 4.4 mm–5.2 mm range, and $\bar{x} = 9.4 \pm 2.67$ SD for specimens in the 5.5 mm–7.6 mm range).

The symphysis of the lower jaw was pigmented at 4.7–4.8 mm; the dorsal surface of the brain was solidly pigmented by 4.7 mm, except for the olfactory lobe region which was pigmented at 5.6 mm. Melanophores were added to the nape to produce a solid blotch by 4.7 mm, the 7.6 mm specimen had a melanistic streak on each side of the snout along the maxillaries, and the upper opercular region was pigmented.

At 4.7 mm, a melanophore was present on the medial surface of each pectoral fin base and small melanophores were scattered over the fin blade. The medial surface of the fin base was solidly

Table 3—Measurements (mm) of larvae of *Sebastes entomelas*.

Body length (age in days)	Yolk sac (length $\times$ width)	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin	
							Length	Base depth
4.6 (1)	0.60 $\times$ 0.45	1.6	0.89	0.22	0.32	0.68	0.21	0.20
4.4 (2)	0.55 $\times$ 0.43	1.5	0.90	0.26	0.31	0.63	0.20	0.20
4.5 (4)	0.45 $\times$ 0.31	1.5	0.92	0.30	0.30	0.62	0.23	0.24
4.5 (7)	0.18 $\times$ 0.18	1.4	0.90	0.26	0.31	0.64	0.25	0.26
4.8 (10)	—	1.6	0.98	0.27	0.33	0.61	0.23	0.24
4.3 (10)	—	1.4	0.85	0.25	0.30	0.59	0.21	0.23

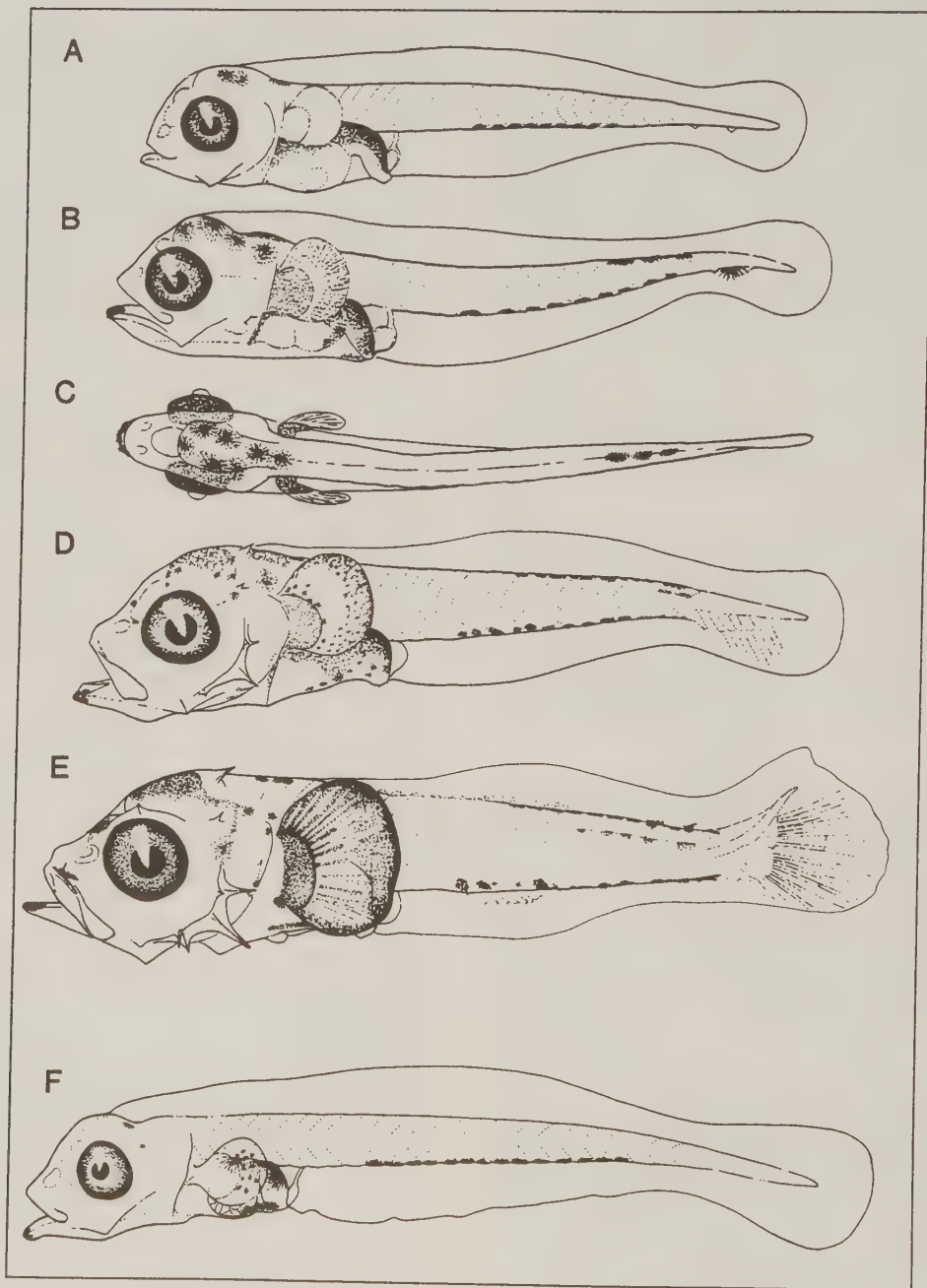


Figure 2—Larvae of *Sebastes rufus* (A-E) and *S. entomelas* (F). A. 4.8 mm, day 3; B. 4.9 mm, day 9; C. 4.9 mm, day 9 (dorsal view); D. 6.1 mm, day 22; E. 7.6 mm, day 35; F. 4.8 mm, day 10.

Table 4—Measurements (mm) of larvae of *Sebastes rufus*.

Body length (age in days)	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin		Pelvic fin length
						Length	Base depth	
4.8 (3)	1.8	1.1	0.29	0.38	0.68	0.25	0.20	
4.8 (4)	1.9	1.2	0.26	0.43	0.81	0.26	0.26	
4.7 (6)	1.8	1.1	0.26	0.42	0.70	0.26	0.26	
4.6 (7)	1.8	1.1	0.31	0.40	0.68	0.25	0.26	
4.8 (8)	1.8	1.2	0.24	0.40	0.70	0.26	0.24	
4.9 (9)	1.9	1.2	0.30	0.48	0.82	0.27	0.34	
5.2 (13)	2.0	1.2	0.29	0.50	0.95	0.34	0.38	
5.6 (13)	2.1	1.2	0.30	0.47	1.0	0.37	0.34	
5.3 (19)	2.0	1.2	0.32	0.50	0.93	0.35	0.39	
5.7 (19)	2.2	1.4	0.44	0.57	1.1	0.48	0.50	
5.9 (19)	2.3	1.5	0.45	0.60	1.2	0.54	0.52	
6.1 (22)	2.6	1.6	0.45	0.66	1.3	0.59	0.52	
*7.6 (35)	3.3	2.2	0.58	0.81	1.7	0.93	0.82	0.05
*7.2 (46)	3.7	2.5	0.65	0.94	1.7	1.0	0.76	0.09

*Specimens undergoing notochord flexion

Table 5—Comparative morphometry (in mm) of preflexion larvae of nine *Sebastes* species ($\bar{x} \pm \text{SD}/\text{range}$).

<i>Sebastes</i> sp.	Snout to anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth
	Body length	Body length	Head length	Head length	Body length	Body length	Body length
<i>constellatus</i>	37.8 $\pm$ 1.30	22.6 $\pm$ 0.89	28.0 $\pm$ 1.87	32.8 $\pm$ 2.49	15.8 $\pm$ 0.84	5.4 $\pm$ 0.55	6.8 $\pm$ 1.30
	36-39	22-24	26-30	29-35	15-17	5-6	5-8
<i>dallii</i>	42.4 $\pm$ 0.52	22.6 $\pm$ 1.06	25.6 $\pm$ 3.02	38.0 $\pm$ 1.85	17.6 $\pm$ 1.85	5.6 $\pm$ 0.52	5.9 $\pm$ 1.36
	42-43	21-24	19-29	35-41	15-20	5-6	3-7
<i>jordanii</i>	36.5 $\pm$ 0.84	22.3 $\pm$ 1.51	26.8 $\pm$ 3.43	37.7 $\pm$ 0.82	17.0 $\pm$ 1.26	6.7 $\pm$ 0.52	6.5 $\pm$ 0.55
	36-38	21-25	23-31	36-38	16-19	6-7	6-7
<i>levis</i>	39.6 $\pm$ 2.30	24.7 $\pm$ 1.60	30.7 $\pm$ 2.63	33.1 $\pm$ 2.67	21.7 $\pm$ 1.11	17.4 $\pm$ 5.29	10.9 $\pm$ 1.57
	37-44	23-28	27-35	29-36	20-23	11-24	8-13
<i>macdonaldi</i>	42.4 $\pm$ 3.53	27.6 $\pm$ 2.25	30.6 $\pm$ 4.16	34.6 $\pm$ 2.34	23.1 $\pm$ 3.99	8.4 $\pm$ 1.21	9.8 $\pm$ 1.48
	36-47	24-31	25-36	31-37	13-27	6-10	8-12
<i>ovalis</i>	38.0 $\pm$ 3.00	23.7 $\pm$ 2.08	21.7 $\pm$ 2.08	38.0 $\pm$ 2.00	16.3 $\pm$ 1.53	6.0 $\pm$ 1.73	7.7 $\pm$ 1.15
	35-41	22-26	20-24	36-40	15-18	5-8	7-9
<i>paucispinus</i>	41.0 $\pm$ 2.74	26.8 $\pm$ 2.28	27.4 $\pm$ 3.21	32.8 $\pm$ 3.77	19.6 $\pm$ 1.67	16.4 $\pm$ 4.56	9.0 $\pm$ 0.71
	37-44	24-29	24-32	29-37	17-21	11-21	8-10
<i>rufus</i>	38.9 $\pm$ 1.44	23.9 $\pm$ 1.38	25.8 $\pm$ 3.19	38.6 $\pm$ 2.97	17.2 $\pm$ 2.18	6.7 $\pm$ 1.67	6.7 $\pm$ 1.67
	38-43	21-26	20-31	35-42	14-21	5-10	4-9
<i>serranoides</i>	36.5 $\pm$ 1.09	22.8 $\pm$ 1.40	28.3 $\pm$ 2.27	37.8 $\pm$ 1.90	15.9 $\pm$ 1.31	5.2 $\pm$ 0.62	6.2 $\pm$ 1.19
	35-38	20-26	25-32	35-41	14-18	4-6	5-8

pigmented by 5.6 mm and the pigment on the blade assumed a distinctive pattern (Fig. 2D, E). Late in the preflexion stage (ca. 6.0 mm), internal melanophores appeared above the dorsal surface of the notochord at the 17th-18th postanal myomeres and extended anteriorly to the 9th myomere in the 7.6-mm specimen (Fig. 2E). A few early larvae had a melanophore in the hypural region (Fig. 2B), but these melanophores did not persist.

Sebastes ovalis

Rearing—Larvae were 4.9-5.1 mm at extrusion and had the oil globule and a small amount of yolk invested in the liver tissue. The yolk persisted to day 5 and the oil globule to day 9. They did not feed on *Brachionus* and *Artemia* nauplii and experienced a massive die-off on day 11. The remaining few were fed wild plankton on day 13 and began to feed, with one specimen living to day 29.

Morphology—The larvae were similar to *S. rufus* (Fig. 3A-C; Tables 5, 6). In the 6.8 mm larva, the caudal rays were forming and the notochord was just beginning to flex. Head spines formed as in *S. rufus*, and the 6.8 mm larva had the following spines: pterotics, parietals, second and fourth anterior preoperculars, and the third posterior preopercular.

Pigmentation—Pigmentation was similar in pattern to that of *S. rufus* larvae but somewhat heavier. The youngest larvae sampled had a patch of 5-8 melanophores above the brain, several melanophores at the nape, a solid sheath above the gut, one or two spots on the medial surface of the pectoral fin base, scattered spots on the fin blade and dorsal and ventral postanal series. The ventral series extended from the fifth or sixth to the 18th or 19th postanal myomeres and contained 13-17 melanophores ($\bar{x} = 14.8 \pm 1.68$ SD for all specimens). The dorsal series was composed of two irregular rows containing 11-12 melanophores in the smallest larvae.

Table 6—Measurements (mm) of larvae of *Sebastes ovalis*, *S. serranoides*, and *S. constellatus*.

Body length (age in days)	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin		Pelvic fin length	Snout anal fin distance
						Length	Base depth		
<i>Sebastes ovalis</i>									
5.1 (5)	1.8	1.1	0.23	0.40	0.79	0.26	0.35		
4.8 (9)	1.8	1.1	0.22	0.44	0.75	0.25	0.34		
6.8 (29)	2.8	1.8	0.44	0.68	1.20	0.54	0.60		
<i>Sebastes serranoides</i>									
4.9 (2)	1.7	1.0	0.31	0.40	0.77	0.25	0.24		
5.0 (2)	1.8	1.1	0.32	0.40	0.74	0.24	0.24		
5.0 (3)	1.8	1.1	0.31	0.40	0.72	0.25	0.25		
5.3 (5)	1.9	1.2	0.33	0.46	0.87	0.27	0.32		
5.2 (7)	1.8	1.2	0.31	0.42	0.71	0.22	0.28		
5.7 (7)	2.1	1.3	0.32	0.47	0.91	0.30	0.36		
5.6 (9)	2.1	1.3	0.36	0.52	1.0	0.33	0.40		
5.8 (12)	2.1	1.3	0.36	0.53	1.0	0.32	0.39		
5.7 (13)	2.1	1.3	0.40	0.50	1.0	0.30	0.40		
5.8 (14)	2.2	1.4	0.45	0.54	0.95	0.32	0.44		
5.8 (16)	2.2	1.5	0.43	0.56	0.95	0.35	0.45		
<i>Sebastes constellatus</i>									
4.5 (4)	1.7	1.0	0.30	0.32	0.75	0.24	0.29		
4.6 (6)	1.8	1.1	0.30	0.32	0.71	0.25	0.30		
4.6 (8)	1.8	1.0	0.26	0.35	0.67	0.27	0.34		
4.4 (9)	1.6	1.0	0.27	0.33	0.72	0.26	0.35		
4.6 (11)	1.7	1.0	0.30	0.35	0.73	0.25	0.35		
*7.1 (38)	3.5	2.3	0.78	0.77	2.0	1.0	0.71	0.30	4.2

*Specimen undergoing notochord flexion

*Specimen undergoing notochord flexion

increasing to 19-21 melanophores in the largest larvae (Fig. 3). Pectoral fin pigmentation was similar to that in *S. rufus*. The tip of the lower jaw became pigmented at about day 9.

Sebastes serranoides

Rearing—Larvae from the two females caught on 18 Jan. 1979 were markedly different in stage of development. Larvae from female #1 were 4.2-4.3 mm long, with a yolk mass of 0.6 mm diameter, and were premature. Larvae from female #2 measured 4.8-5.4 mm, had no yolk and only a remnant of the oil globule in the liver tissue. These larvae began feeding immediately on wild plankton whereas the premature brood began feeding on day 5, when only a remnant of yolk was visible in the liver tissue. Both groups had massive die-offs due to improper water circulation and stratification on day 9; however, a few larvae from both broods survived to day 16.

Morphology—The larvae were similar to *S. rufus* (Fig. 3D-F; Tables 5, 6). Caudal fin rays were not forming in the largest specimens, nor were head spines.

Pigmentation—Pigmentation was similar to that of *S. rufus*. In a sample of 30 newborn larvae from female #1, 17% lacked pigment over the brain, 73% had 1 or 2 melanophores, and 10% had 3-4 melanophores above the brain. Nape melanophores were lacking in 57% of the larvae, 33% had one nape spot, and 10% had 2-3 spots. By day 5, melanophores covered the brain and nape. Newborn larvae had a melanistic shield over the gut and a distinct series of melanophores along the ventral midline below the gut. All newborn larvae had a melanophore at the future hypural region. The postanal ventral midline series extended from the third or fourth postanal myomere to the 18th-20th and contained 14-20 melanophores ($\bar{x} = 16.0 \pm 1.60$ SD for the entire growth series). Of 100

newborn larvae examined, 67 lacked dorsal midline melanophores, 28 had a single melanophore, and 5 specimens had 2 melanophores at the 17th-19th postanal myomeres. At the end of the first week, additional melanophores appeared in the dorsal midline series and 9 to 14 day larvae had 7-16 ($\bar{x} = 13.2 \pm 3.70$ SD) melanophores in the series.

At day 5, the tip of the lower jaw and the pectoral fins were pigmented. The medial surface of the pectoral fin base had a large melanophore and the outer half of the fin blade had a covering of fine melanophores. By day 9 the medial surface of the fin blade was fully pigmented and the fin blade had a distinct pigment pattern (Fig. 3E). Also, at this stage melanophores appeared on the snout, opercular region, and lateral nape region. At day 14 the medial surface of the fin base was totally pigmented.

Sebastes constellatus

Rearing—Newborn larvae of *S. constellatus* were 4.0-5.0 mm at extrusion, had a small remnant of the oil globule, and began feeding immediately on wild plankton. There was a massive die-off at the end of the first week and the single larva remaining alive at the end of the second week lived to day 38.

Morphology—Early larvae of *S. constellatus* were morphologically indistinct (Fig. 4A-C; Tables 5, 6). The 38-day specimen (7.1 mm) was similar to larvae of other species of the subgenus *Sebastomus* (Moser et al. 1977; Richardson and Laroche 1979), in having a relatively large head with strong spination and the following head spines: second and third anterior preoperculars, second and fourth posterior preoperculars, pterotics, posttemporals, postoculars, and parietals. Each postocular spine was borne on a prominent supraocular shelf, and the heavily serrated parietals were elongated compared with those of *S. rufus*. Also, in this specimen the dorsal and anal fin bases and the pelvic fins were beginning to form.

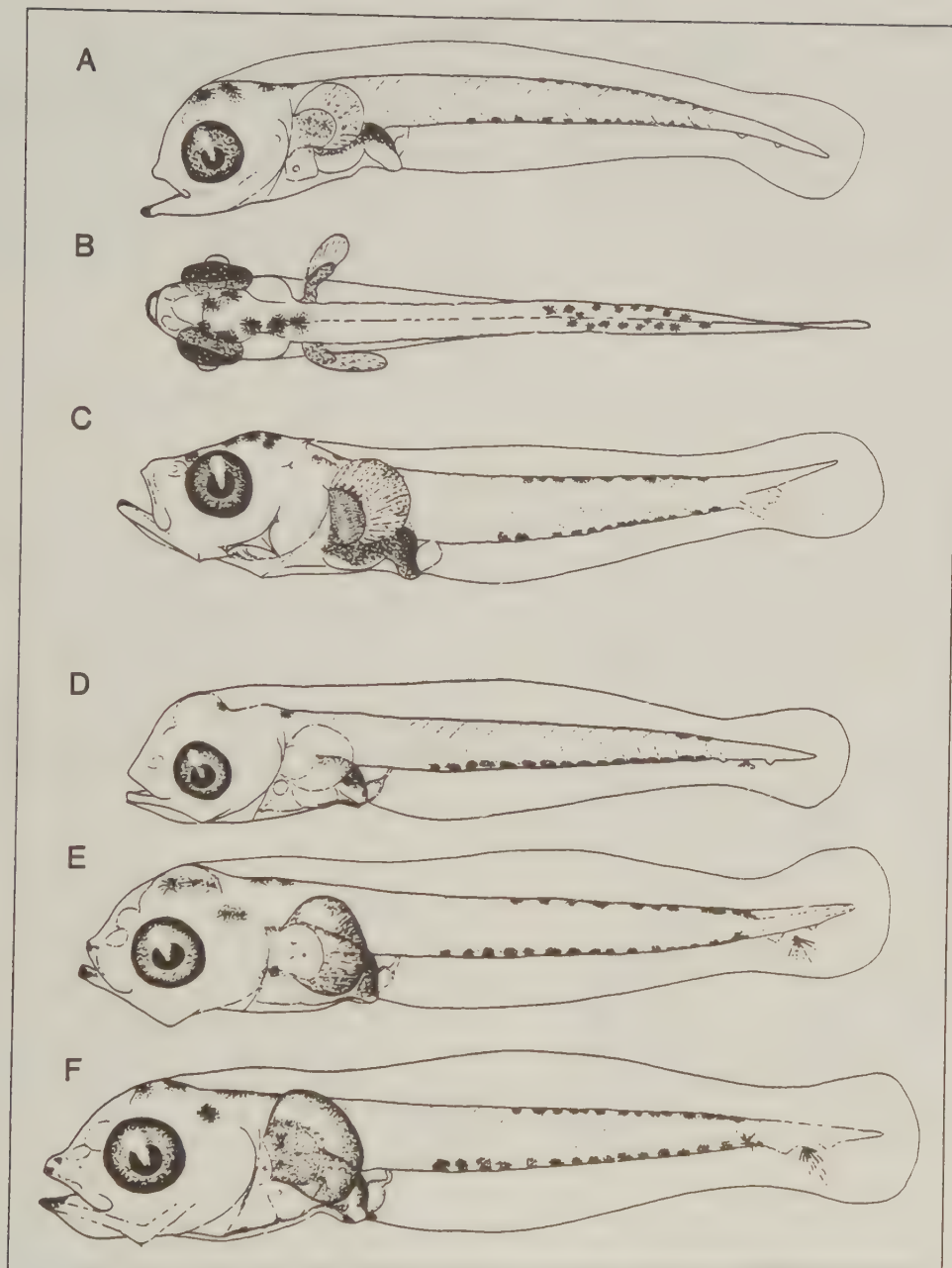


Figure 3—Larvae of *Sebastes ovalis* (A-C) and *S. serranoides* (D-F). A. 4.9 mm, day 9; B. 4.9 mm, day 9 (dorsal view); C. 6.8 mm, day 29; D. 5.0 mm, day 2; E. 5.6 mm, day 9; F. 5.8 mm, day 14.

Pigmentation—Pigmentation in early larvae of *S. constellatus* was similar to that known for other species of *Sebastomus*. The pigment pattern consisted of a spot at the tip of the lower jaw, a shield over the gut, a ventral midline series below the gut, and a postanal ventral series extending from the third to the 15th postanal myomere and containing 12-16 melanophores (Fig. 4). During the first week, the pectoral fin blade became covered with small melanophores that were denser at the distal margin. The 7.1-mm larva had snout pigment, a covering of melanophores above the brain, nape spots, a solidly pigmented pectoral fin-base, pelvic fin pigment, and a hypural spot (Fig. 4C). Dorsal midline pigment was not present.

Sebastes rubrivinctus

Rearing—The brood of larvae collected on 15 Sept. 1976 was held at two temperature ranges, 8.8-9.3°C and 14.4-15.0°C, to provide specimens for sinking rate experiments, and were not fed subsequently. After two weeks, the least advanced individuals were about 4.8 mm long, had a yolk sac measuring about 0.6×0.7 mm, and an oil globule about 0.23 mm in diameter; the most advanced specimens lacked yolk and had an oil globule 0.10-0.20 mm in diameter. Sinking rates ranged from 0.6 cm/s for the least advanced to 0.09 cm/s for the most advanced (Table 7, Fig. 5).

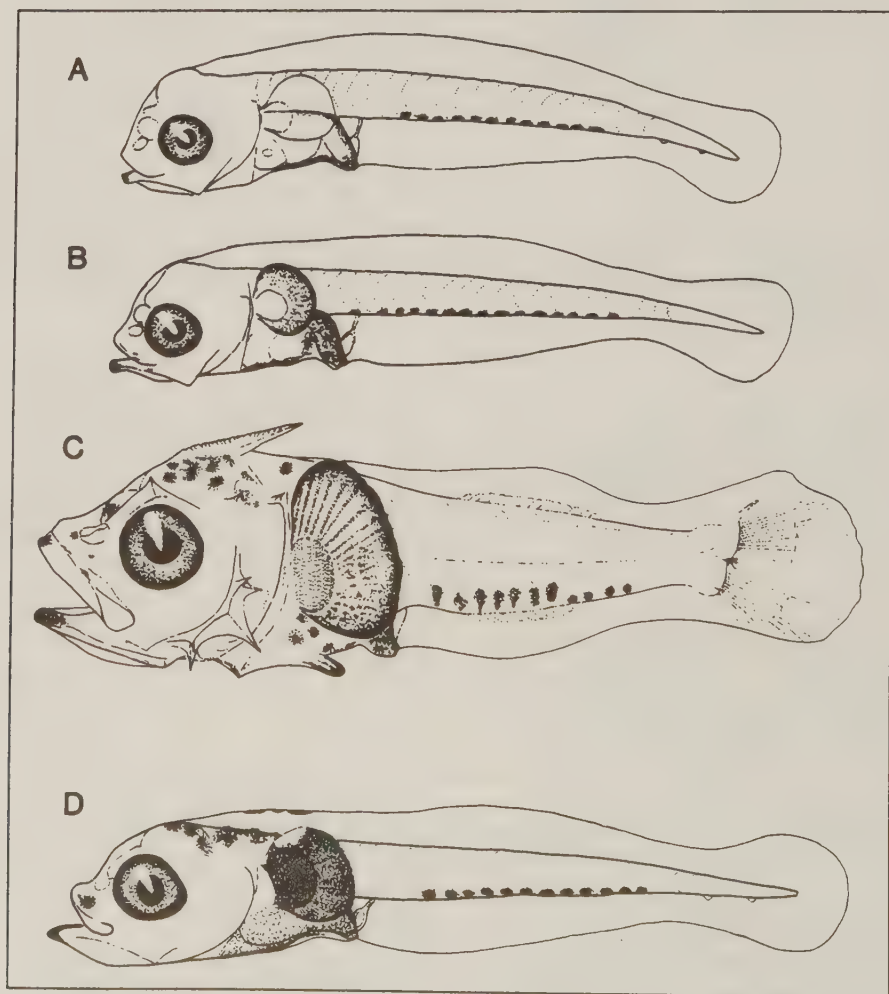


Figure 4—Reared larvae of *Sebastes constellatus* (A-C) and *S. rubrivinctus* (D). A. 4.5 mm, day 4; B. 4.6 mm, day 11; C. 7.1 mm, day 38; D. 5.1 mm, day 14.

Table 7—Sinking rates for anesthetized larvae of *Sebastes rubrivinctus* at different stages of yolk and oil globule utilization.

Specimen length (mm)	Yolk			Oil globule diameter (mm)	Sinking time (min:s)	Beaker height (cm)	Sinking rate (cm/s)
	length (mm)	width (mm)	volume (mm ³)				
4.8	0.70	0.60	0.154	0.23	0:59.8	36.5	0.61
4.9	0.74	0.58	0.166	0.22	1:44.8	36.5	0.35
4.8	0.64	0.54	0.116	—	1:54.2	36.5	0.32
5.0	0.68	0.50	0.121	0.24	2:26.6	36.5	0.25
5.1	0.46	0.30	0.033	0.18	3:06.8	36.5	0.20
5.0	0.38	0.30	0.023	0.20	3:11.2	36.5	0.19
5.2	0.56	0.36	0.059	0.20	3:20.4	36.5	0.18
5.2	0.38	0.32	0.024	—	3:24.0	36.5	0.18
5.0	0.38	0.26	0.020	0.24	3:32.4	36.5	0.17
4.8	0	0	0	0.10	4:26.6	36.5	0.14
5.1	0	0	0	0.12	6:45.0	36.5	0.09
4.8	0.08	0.08	<0.001	0.20	7:05.8	36.5	0.09

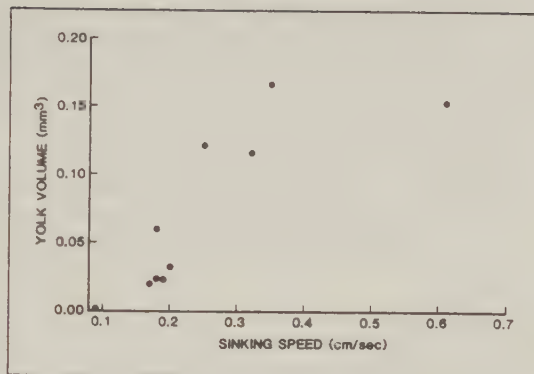


Figure 5—Sinking speed of larvae of *Sebastes rubrivinctus* at various stages of yolk utilization.

Pigmentation—In yolk-exhausted larvae, the head was heavily pigmented with melanophores covering the brain, nape, lower jaw, and with one or more melanophores in the snout (Fig. 4D). One to several melanophores were present at the margin of the dorsal finfold above the nape. Finfold pigmentation has not been reported in larvae of other species of *Sebastes*. The median surface of the pectoral fin base was covered solidly with melanophores as was the blade, except for a small dorsally located clear zone. The gut was pigmented solidly on all surfaces. Postanal pigmentation consisted of a ventral midline series of 13-23 melanophores ($\bar{x} = 16.4 \pm 1.82$ SD for 50 specimens) extending from the third or fourth postanal myomere to the 15th-16th.

DISCUSSION

Our ability to identify the early-stage larvae of rockfishes has progressed so that, for some species, standard plankton surveys may be used to determine the temporal and areal extent of spawning and relative larval abundance (Moser et al. 1977). These surveys also provide the possibility for estimation of spawning biomass when critical information on fecundity, larval mortality, and duration of the early pelagic phase becomes available. The species with identifiable larvae are only a fraction of the rockfish species which are currently or potentially important to fisheries. Larval series which have been described have distinctive morphological features, pigmentation, temporal and spatial distributions, or a combination of these characters, and are readily identifiable compared with the unidentified species which have more subtle larval characters. Rearing of larval series provides the means for increasing the number of identifiable species; however, rockfish are difficult to rear. We have not been able to duplicate the Japanese success with *Artemia* as a food (Table 1) largely because eastern Pacific species are smaller and comparatively less developed at birth (Table 1) and we have had to rely on freshly collected wild plankton. Indeed, in our rearing attempts, high concentrations of *Brachionus* have not elicited feeding behavior. The recent successful rearing of copper and brown rockfish (*S. caurinus* and *S. auriculatus*) larvae to the stage of caudal fin formation on a diet of *Brachionus* and *Artemia* (Stahl-Johnson 1985) suggests a diversity in larval food requirements among eastern Pacific species.

The number and arrangement of postanal midline pigment series

have been emphasized as key characters in identifying rockfish larvae (DeLacy et al. 1964; Moser 1967; Westrheim 1975; Moser et al. 1977). Previously, early-stage rockfish larvae have been divided into two groups: those with both dorsal and ventral midline series and those with only ventral series. Larvae of *S. rufus* and *S. seranoides*, described herein, represent a third type which has only a ventral midline series at birth (most specimens) but soon develops a substantial dorsal midline series to which melanophores are added gradually. This must also happen in *S. entomelas* and *S. flavidus*, since newborn larvae lack dorsal midline series (Westrheim 1975) but early postflexion larvae (Laroche and Richardson 1980, 1981) have well developed dorsal midline series. The usefulness of the postanal pigment series as a larval character will depend on knowing the composition and arrangement of these series at precise developmental stages, knowledge which can be obtained only by rearing each species.

The distribution of dorsal and ventral midline pigment may provide characters for systematic analysis. Barsukov (1981) has hypothesized that the widow rockfish (*S. entomelas*) is most closely related to the blue rockfish (*S. mystinus*) and that these two are part of a group that includes *S. flavidus*, *S. melanops*, and *S. seranoides*. Also, Barsukov proposed that the sister group to the *S. entomelas* group includes *S. rufus*, *S. ovalis*, and *S. hopkinsi*. Characters of first-feeding larvae are now known for all of the above species. In the former group and *S. rufus*, first-feeding larvae have only a ventral row of postanal midline pigment but develop a dorsal row during the preflexion larval stage (not known for *S. mystinus*). First-feeding larvae of *S. ovalis* and *S. hopkinsi* have both dorsal and ventral postanal midline pigment. More precise knowledge of the number and arrangement of postanal midline pigment is needed to test the utility of this character in species identification and systematic analysis.

The larvae of the starry rockfish, *S. constellatus*, show the suite of pigment and morphological characters described for other members of the subgenus *Sebastomus* (Moser et al. 1977; Richardson and Laroche 1979). Preflexion and postflexion larvae of this group have a postanal ventral midline series only and pigment on the dorsal head region, on the lower jaw, and on the pectoral fins (heaviest on the distal margin). Late in the postflexion stage, *Sebastomus* larvae develop a blotch on the caudal peduncle and a saddle beneath the spinous dorsal fin. It is likely that early larval stages of this group will not be identifiable to species. In groups

such as these, the late larval and pelagic juvenile stages could be used to estimate recruitment, depending on our ability to sample these stages adequately. Mid- and late-stage larvae are undersampled by plankton nets (Fig. 1) and juvenile habitats are diverse for the large array of *Sebastes* species. Those with distinct pelagic juvenile stages could be sampled with midwater trawls, surface nets, or small-mesh purse seines depending on their location in the water column (Moser and Ahlstrom 1978; Laroche and Richardson 1981). Those species which transform and quickly settle to soft-bottom habitats can be sampled by small-mesh bottom trawls; however, those which settle quickly to rocky habitats may be vulnerable only to traps.

An important aspect of the life history of rockfish was addressed by the sinking rate experiment on *S. rubrivinctus* larvae reported in this paper. The sinking rate in rockfish embryos and yolked larvae decreases with decreasing yolk volume (Fig. 5), whereas in species with pelagic eggs such as the plaice (Blaxter and Ehrlich 1974) and the northern anchovy (Hunter and Sanchez 1976) sinking rate increases with decreasing yolk volume. Whereas the newly hatched larvae of fish species with pelagic eggs find themselves positioned or maintained in the upper water column by virtue of their buoyant eggs, all evidence indicates that rockfish larvae are extruded at the depth range of the adults and rise to the upper water column. Since prematurely born yolk-sac larvae would sink rapidly to the bottom and die, birth must be coordinated precisely with the time of yolk and oil globule exhaustion. Perhaps birth is initiated by behavioral or biochemical cues from the full-term larvae. If birth was initiated by the female, she would gain some latitude in the critical timing of extrusion, particularly if she were able to provide nutrition to the developing brood after yolk exhaustion. Indeed, maternal nutrition is suggested by the markedly greater rearing success of broods spawned spontaneously by captive females compared with broods taken from field-caught females. Recently, Boehlert and Yoklavich (1984) have demonstrated maternal nutrition in *Sebastes*.

Early mortality in *Sebastes* follows a vastly different path than in other fishes with a prolific larval stage. Rockfish have avoided the high mortality of the egg stage (e.g., 30-40%/day for northern anchovy reported by Stauffer and Picquelle 1980) since there is insignificant intraovarian mortality, even in species with brood sizes exceeding 2 million embryos (Moser 1967). The great reproductive potential inherent in being able to produce large numbers of fully-formed larvae that are ready to feed on zooplankters is balanced by the mortality encountered in the journey of these first-feeding larvae from their place of birth to the upper water column. This mortality is controlled to some degree by events during late intraovarian life since survival of newborn young depends on their state of organ development, energy reserves, and buoyancy. Studies on intraovarian physiology of *Sebastes* (Boehlert and Yoklavich 1984) and attention to brood condition in field-caught females will provide valuable insight into rockfish production.

ACKNOWLEDGMENTS

We are indebted to Richard Pleasant for supplying larvae of *S. rufus*, *S. ovalis*, and *S. constellatus* and to William Flerx for supplying larvae of *S. serranoides*. Assistance during the rearing was provided by Morgan Busby, Susan D'Vincent, Barbara MacCall, Elaine Sandknop, and Elizabeth Stevens. Eric Lynn provided cultures of algae, *Brachionus*, and *Tisbe*. We thank Mary DeWitt for typing the manuscript. The senior author would like to give special acknowledgment for the help provided by the late David Kramer during the sinking rate experiment and for his assistance and companionship on many rockfish collecting trips.

CITATIONS

- AHLSTROM, E. H.
1954. Distribution and abundance of egg and larval populations of the Pacific sardine. *Fish. Bull.*, U.S. 56:83-140.
1961. Distribution and relative abundance of rockfish (*Sebastes* spp.) larvae off California and Baja Calif. *Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer* 150:169-176.
1966. Distribution and abundance of sardine and anchovy larvae in the California Current Region off California and Baja California, 1951-64: a summary. *U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish.* 534, 71 p.
1968. An evaluation of the fishery resources available to California fishermen. In D. Gilbert (ed.), *The future of the fishing industry of the United States*. Univ. Wash. Publ. Fish., New Ser. 4:65-80.
AHLSTROM, E. H., H. G. MOSER, and E. M. SANDKNOP.
1978. Distributional atlas of fish larvae in the California Current Region: Rockfishes, *Sebastes* spp.: 1950 through 1975. *Calif. Coop. Oceanic Fish. Invest. Atlas* 26, 178 p.
BARSUKOV, V. V.
1981. A brief review of the subfamily Sebastinae. *J. Ichthyol.* 21(1):1-26.
BOEHLERT, G. W., and M. M. YOKLAVICH.
1984. Reproduction, embryonic energetics, and the maternal-fetal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). *Biol. Bull. (Woods Hole)* 167:354-370.
BLAXTER, J. H. S., and K. F. EHRLICH.
1974. Changes in behavior during starvation of herring and plaice larvae. In J. H. S. Blaxter (ed.), *The early life history of fish*, p. 575-588. Springer-Verlag, N.Y.
DeLACY, A. C., C. R. HITZ, and R. L. DRYFOOS.
1964. Maturation, generation, and birth of rockfish (*Sebastes*) from Washington and adjacent waters. *Wash. Dep. Fish., Fish. Res. Pap.* 2(3):51-67.
FUJITA, S.
1957. On the larval stages of a scorpaenid fish, *Sebastes pachycephalus nigricans* (Schmidt). [In Jpn., Engl. summ.] *Jpn. J. Ichthyol.* 6:91-93.
1958. On the egg development and larval stages of a viviparous scorpaenid fish, *Sebastes oblongus* Gunther. [In Jpn., Engl. summ.] *Bull. Jpn. Soc. Sci. Fish.* 24:475-479.
HUBBS, C. L., W. I. FOLLETT, and L. J. DEMSTER.
1979. List of the fishes of California. *Occas. Pap. Calif. Acad. Sci.* 133, 51 p.
HUNTER, J. R., and C. SANCHEZ.
1976. Diel changes in swim bladder inflation of the larvae of the northern anchovy, *Engraulis mordax*. *Fish. Bull.*, U.S. 74:847-855.
KUSAKARI, M., Y. MORI, and K. KUDO.
1977. Studies on the breeding habit of a rockfish, *S. schlegelii* (Hilgendorf). 2. On the breeding behavior of pregnant fish and the just spawned larvae. *Geppo, Hokkaido Fish. Exp. Stn.* 34(10):1-11.
LAROCHÉ, W. A., and S. L. RICHARDSON.
1980. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes flavidus* and *Sebastes melanops* (Scorpaenidae) off Oregon. *Fish. Bull.*, U.S. 77:901-924.
1981. Development of larvae and juveniles of the rockfishes *Sebastes entomelas* and *S. zacentrus* (Family Scorpaenidae) and occurrence off Oregon, with notes on head spines of *S. mystinus*, *S. flavidus* and *S. melanops*. *Fish. Bull.*, U.S. 79(2):231-257.
MOSER, H. G.
1967. Reproduction and development of *Sebastes paucispinis* and comparison with other rockfishes off southern California. *Copeia* 1967:773-797.

- MOSER, H. G., and E. H. AHLSTROM.
1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Board Can. 35:981-996.
- MOSER, H. G., E. H. AHLSTROM, and E. M. SANDKNOP.
1977. Guide to the identification of scorpionfish larvae (Family Scorpaenidae) in the eastern Pacific with comparative notes on species of *Sebastes* and *Helicolenus* from other oceans. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 402, 71 p.
- MOSER, H. G., and J. L. BUTLER.
1981. Description of reared larvae and early juveniles of the calico rockfish, *Sebastes dallii*. Calif. Coop. Oceanic Fish. Invest. Rep. 22:88-95.
- MOSER, H. G., E. M. SANDKNOP, and D. A. AMBROSE.
1985. Larvae and juveniles of aurora rockfish, *Sebastes aurora*, from off California and Baja California. In Kendall, A. W., Jr., and J. B. Mariave (eds.), Descriptions of early life history stages of selected fishes, p. 55-64. Can. Tech. Rep. Fish. Aquat. Sci. 1359.
- RICHARDSON, S. L., and W. A. LAROCHE.
1979. Development and occurrence of larvae and juveniles of the rockfishes, *Sebastes crameri*, *Sebastes piniger* and *Sebastes helvomaculatus* (Family Scorpaenidae) off Oregon. Fish. Bull., U.S. 77:1-41.
- SIKAWA, T., and H. TSUKAHARA.
1961. Studies on habits of coastal fishes in the Amakusa Islands. I. Early life history of the purple rockfish, *Sebastes pachycephalus pachycephalus* Temminck et Schlegel. Rec. Oceanogr. Works Jpn., Spec. No. 5:123-127.
- SMITH, P. E.
1972. The increase in spawning biomass of northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:849-874.
- STAHL-JOHNSON, K. L.
1985. Descriptive characteristics of reared *Sebastes caurinus* and *S. auricularis* larvae. In Kendall, A. W., Jr., and J. B. Mariave (eds.), Descriptions of early life history stages of selected fishes, p. 65-76. Can. Tech. Rep. Fish. Aquat. Sci. 1359.
- STAUFFER, G. D., and S. J. PICQUELLE.
1980. Estimates of the 1980 spawning biomass of the central subpopulation of northern anchovy. Admin. Rep. LJ-80-09, Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, Ca, 42 p.
- TSUKAHARA, H.
1962. Studies on habits of coastal fishes in the Amakusa Islands. Part 2. Early life history of the rockfish *Sebastes marmoratus* (Cuvier and Valenciennes). Rec. Oceanogr. Works Jpn., Spec. No. 6:49-55.
- WESTRHEIM, J. J.
1975. Reproduction, maturation, and identification of larvae of some *Sebastes* (Scorpaenidae) species in the northeast Pacific Ocean. J. Fish. Res. Board Can. 32:2399-2411.

LARVAL FISH ASSEMBLAGES IN THE CALIFORNIA CURRENT REGION, 1954-1960, A PERIOD OF DYNAMIC ENVIRONMENTAL CHANGE

H. GEOFFREY MOSER, PAUL E. SMITH, AND LAWRENCE E. EBER

National Marine Fisheries Service
 Southwest Fisheries Center
 P. O. Box 271
 La Jolla, California 92038

ABSTRACT

Analysis of nearly 200 taxa of fish larvae from CalCOFI surveys in 1954-60 placed 30 taxa into nine recurrent groups. Two complexes of four recurrent groups each were formed by extensive interlinking among the groups. A "northern" complex represents the subarctic-transitional fauna and the coastal pelagic fauna and its associates. A "southern" complex incorporates transitional, warm-water cosmopolite and eastern tropical Pacific taxa. One recurrent group was associated with the extensive continental shelf area of Bahía Sebastián Viscaíno and the Punta Abreojos-Cabo San Lázaro Bight. Oceanographic changes between the cold 1955-56 period and the warm 1958-59 period changed the boundary between the two pelagic complexes and altered the onshore-offshore distribution of the fauna. There was much variability in the constitution of the recurrent groups within the complexes and some change in the degree of overlapping species distributions among the complexes over the seven-year period from 1954 to 1960. The northern-southern complex structure was similar to that described in a previous analysis of data from 1975.

RESUMEN

El análisis de casi 200 taxa de larvas de peces colectados por CalCOFI durante los años 1954-60 ubicó 30 taxa en nueve grupos recurrentes. Extensas interrelaciones entre los grupos recurrentes dieron como resultado dos complejos con cuatro grupos recurrentes cada uno. Un complejo "norteño" representa la fauna subártica-transicional y la fauna pelágica costera y sus asociados. Un complejo "sureño" incorpora taxa cosmopolitas transicionales de aguas cálidas y taxa del este del Pacífico tropical. Un grupo recurrente está asociado con la extensa plataforma continental en el área de las bahías Sebastián Vizcaíno y Punta Abreojos-Cabo San Lázaro. Los cambios oceanográficos ocurridos entre el período frío de 1955-56 y el período cálido de 1958-59 modificaron el límite entre

los dos complejos pelágicos y alteraron la distribución perpendicular a la costa de la fauna. Durante un período de siete años, 1954-60, la formación de los grupos recurrentes dentro de los complejos presentó gran variabilidad; a la vez, se observó algunos cambios en el grado de superposición de las distribuciones de especies entre los complejos. La estructura norte-sur de los complejos es similar a aquella descrita en un previo análisis de datos.

INTRODUCTION

A principal task of ecologists is to define the boundaries of communities. In pelagic ecology the task is made difficult by fluid boundaries controlled by meteorological, bathymetric, and oceanographic factors. The composition and structure of planktonic and nektonic communities of the California Current and adjoining regions have been studied extensively over the past 50 years. Broad-scale community analyses (Fager and McGowan 1963; McGowan 1971) and distributional studies (Brinton 1962; Ebeling 1962; Alvarino 1964; Reid et al. 1978) showed that water masses in the North Pacific have highly characteristic faunas, confirming the findings of earlier workers (see Sverdrup et al. 1942; Ekman 1953). Subsequent distributional and community studies provided additional faunal definitions of these water masses: central—McGowan and Walker (1979), Venrick (1979), Loeb (1979, 1980), Barnett (1983, 1984); eastern tropical Pacific—Ahlstrom (1971, 1972a), Brinton (1979); subarctic—Parin (1961), Richardson and Percy (1977), Richardson et al. (1980), Kendall and Clark (1982), Willis (1984).

The transitional nature of the California Current region is reflected in its fauna, which is a mixture of species that occur in adjacent water masses, and some endemic species (Figure 1). The fish fauna has been studied intensively, leading to community analyses of the nearshore environment (Horn and Allen 1978; Allen 1985); the Southern California Bight region (Gruber et al. 1982); the coastal demersal habitat (Mearns 1974; Allen 1982); and the offshore mesopelagic zone (Ebeling et al. 1970). Loeb et al. (1983) examined the composition and structure of the ichthyoplankton occurring in the

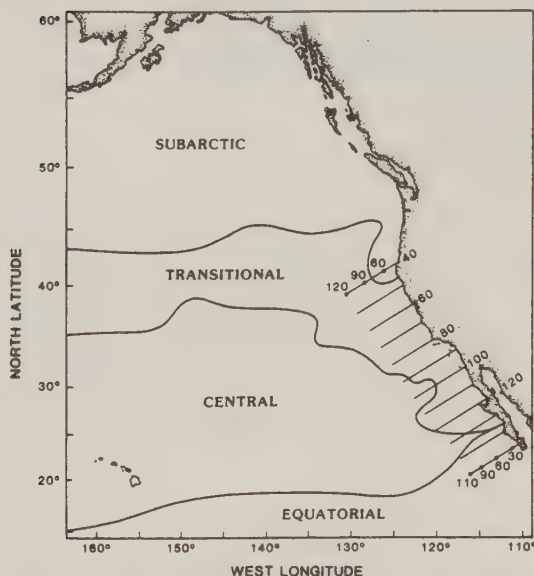


Figure 1. Four major zoogeographic zones in the northeast Pacific as defined by Brinton (1962). The boundaries represent the 50% margins of incidence of the euphausiid shrimp species that characterize these faunal zones. Cardinal lines and selected stations of the basic CalCOFI sampling pattern are shown.

California Cooperative Oceanic Fisheries Investigations (CalCOFI) sampling area during 1975.

This paper is the first step in analyzing community dynamics over the entire CalCOFI time series, from 1949 to the present. Recent progress in establishing a computer data base for CalCOFI ichthyoplankton time series has allowed us to study the seven-year period from 1954-60, which was characterized by maximum areal and seasonal sampling coverage during a sequence of anomalously cold and warm oceanographic regimes. In this paper we describe the ichthyoplankton assemblages of the California Current region represented by the 1954-60 data base and examine the changes in these assemblages in relation to major oceanographic changes during that period.

Interannual and seasonal oceanographic changes in the California Current region have been studied extensively (Reid 1960; Chelton 1981; Lynn and Simpson, in press), and much attention has been directed to how these changes affect the distribution and abundance of organisms (Bakun 1985; Bakun and Parrish 1982; Chelton et al. 1982; Fiedler et al. 1986; Lasker 1978; Mullin and Brooks 1970; Smith 1985; Smith and Eppley 1982; Smith and Lasker 1978). For our analysis we assembled the CalCOFI oceanographic data from the 1954-60 period into unique sets of files. This

allowed us to describe oceanographic changes in relation to changes in larval fish assemblages and their component taxa.

MATERIALS AND METHODS

This study was based on 907,000 fish larvae from 11,500 plankton net tows taken on annual CalCOFI surveys during the seven-year period from 1954 to 1960. Larvae were identified to species or the lowest taxon possible. Of 191 taxa there were 97 species and 39 generic, 51 familial, and 9 ordinal categories. The distribution of taxonomic categories differs from the original set because identifications were improved during the editing and verification of the data base (Ambrose et al., in press a, b; Sandknop et al., in press; Stevens et al. in press a, b; Sumida et al., in press a, b).

Detailed descriptions of the field and laboratory methods employed in sampling the fish larvae used in this study were described in Kramer et al. (1972). Almost all samples can be associated with 10-m temperature and salinity data taken from the same ship within the hour and within hundreds of meters. (Anon. 1963) Geostrophic flow has been analyzed from most of these cruises from approximately a third of the stations (Wyllie 1966).

In this study, larval fish assemblages were described by recurrent group analysis (Fager 1957, 1963; Fager and McGowan 1963). This analysis determines groups of taxa that occur together relatively frequently and are consistently part of each other's environment. Two major procedures are involved in the analysis—the calculation of an index of affinity (program name AFFINITY) for each pair of taxa that ever occur together in a plankton sample, and the formation of groups of taxa (program name REGROUP) based on a chosen minimum index value (0.3 for this work)¹. The category "group member" is supplemented by the term "associate" for taxa that have significant affinity indices with one or more but not all group members in one or more groups, and "affiliate" for any remaining taxon that is related to a group by having its highest affinity index (always < 0.3) with a group member. To gain a hierarchical view of the relationships of the principal taxa, the REGROUP procedure was applied to the combined 1954-60 data set at three higher critical affinity levels (0.4, 0.5, and 0.6).

The equation for the affinity index is:

$$I = \frac{N_{ij}}{\sqrt{N_{ii} \cdot N_{jj}}} - \frac{1}{2 \cdot \sqrt{N_{ii} \cdot N_{jj}}}$$

¹Programs, written in Turbo-Pascal, are available from the authors.

where I is the affinity index,

N_j is the number of joint occurrences;

N_a is the number of occurrences of taxon a,
the less common taxon, and

N_b is the number of occurrences of taxon b,
the more common taxon.

The second term in the equation is a correction factor, which adjusts the affinity index according to the sample size. The correction factor is small for the more common taxa. The first term is the geometric mean coincidence. The consequence of the correction factor is that a pair of organisms would have to coincide 52% of the time to have an affinity index of 0.3 if number of occurrences of the commoner taxon were 5; 37% of the time if the number of occurrences of the commoner taxon were 50; but only 31% of the time if the number of occurrences of the commoner taxon were 5,000.

The oceanographic data used in this study are a compilation of physical and chemical observations made in conjunction with the plankton net tows on CalCOFI survey cruises. The data were processed by the Scripps Institution of Oceanography and published in a series of data reports (cited in Eber and Wiley 1982). For the purpose of documenting the changes in oceanic conditions that occurred during the 1957-59 El Niño, the CalCOFI oceanographic data were separated into two periods: 1955-56 (13 cruises) and 1958-59 (24 cruises).

Over much of the region, the largest differences between the two periods did not occur at the surface, but at depths varying from 30 to 100 meters. Therefore, rather than selecting discrete depths for this overview, we computed averages of oceanographic parameters for the upper 100 meters using data from five standard depths: 10, 30, 50, 75, and 100 meters. For mapping the parameters, we rejected stations at locations where depth to bottom was less than 100 meters to avoid bias associated with vertical gradients. We used harmonic coefficients to compute mean values for oceanographic parameters at each CalCOFI station. These coefficients, based on data from all CalCOFI cruises from 1950 to 1978, were computed for each CalCOFI station by the method of least squares fit to a mean annual cycle.

Anomalies of oceanographic parameters for standard depths on individual CalCOFI cruises were determined by computing deviations from the harmonic means. Anomalies of temperature and salinity were obtained in this way for cruises in each of the selected periods. We analyzed each

group of anomalies on a two-dimensional grid fitted to the CalCOFI station pattern. We then subtracted the grid, or matrix, of 1955-56 anomalies from that for the 1958-59 anomalies to obtain charts of differences between the periods.

We examined the association between species distribution and oceanographic characteristics in two adjacent offshore areas of the CalCOFI survey region, between Point Conception, California, and Punta Eugenia, Baja California. These areas include that portion of the CalCOFI station pattern between lines 80 and 120, separated by line 100. The northern area is in the southern fringe of the habitat of two subarctic-transition species, *Stenobrachius leucopsarus* and *Tarletonbeania crenularis*. The southern area is in the northern fringe of the habitat of two eastern tropical Pacific species, *Vinciguerrria lucetia* and *Diogenichthys laternatus* (Moser and Ahlstrom 1970; Ahlstrom 1972b). CalCOFI net-tow data from cruises conducted during 1954-56 and 1958-60 were scanned for occurrences of these species in the respective areas.

The data for each of the four species were separated into two categories, one representing samples containing no larvae of the targeted species and the other representing samples containing larvae in excess of a fixed threshold number for each species. The threshold (positive) counts were 10 for *S. leucopsarus* and *V. lucetia*, and 3 for *T. crenularis* and *D. laternatus*. The CalCOFI station codes and cruise dates for each category were then used to separate the oceanographic data into two corresponding groups for each species.

The purpose of this exercise was to test whether the presence or absence of these species provided sufficient criteria to partition the oceanographic data into distinctively different groups. Accordingly, all of the data collected at each station within each area were combined into two temperature-salinity profiles for each species, corresponding to the two categories of larval occurrence (zero or positive). After discarding those stations not represented by both categories (for each species), to avoid geographical bias, we combined the station profiles into a single pair of area profiles for each species.

OCEANOGRAPHY

General Description

The California Current region is bordered by three water masses: subarctic to the north, Pacific central to the west, and equatorial to the south (Tsuchiya 1982). The California Current begins as

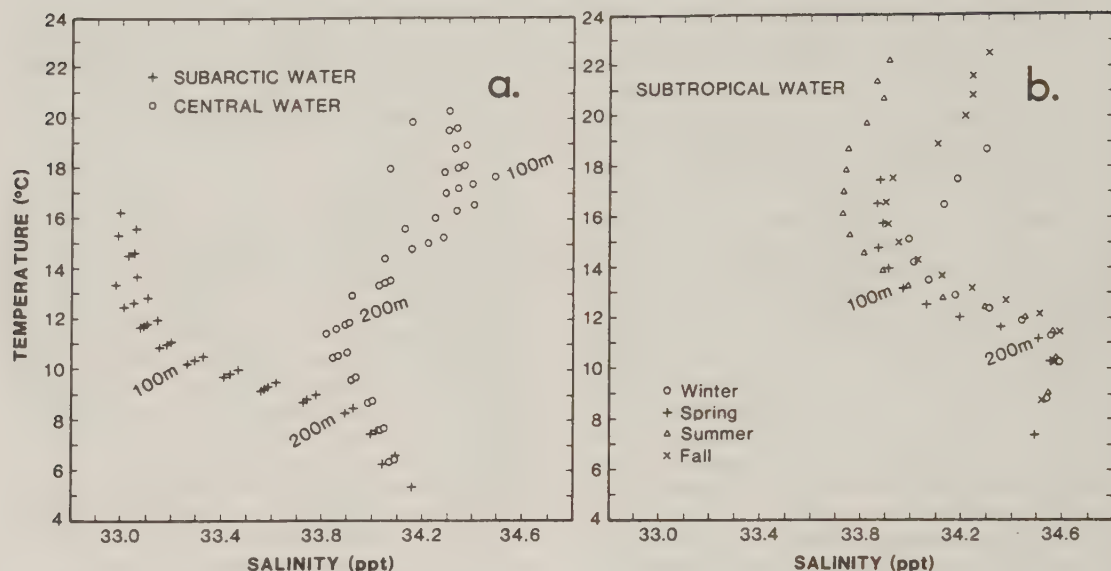


Figure 2. Mean seasonal temperature-salinity plots for modified subarctic water and Pacific central water (a) and subtropical water (b) in the California Current region. The symbols are plotted for discrete values of sigma-t at intervals of 0.2 g/l.

the southward-turning branch of the transpacific West Wind Drift, with characteristics of subarctic water. As the current proceeds southeastward, these characteristics are modified by excess heating, evaporation, and by intrusion of water from the west and south (Hickey 1979). Further modification is caused by entrainment of mesoscale eddies of upwelled water from coastal areas (Lynn and Simpson, in press).

The peripheral water masses' influence on California Current water can be seen in mean temperature-salinity (T-S) relationships in the upper few hundred meters at different locations (Figure 2). The symbols on the T-S curves were plotted at constant intervals of sigma-t (0.2 g/l). Each symbol represents a seasonal mean, so that their spread along constant sigma-t lines is a measure of seasonal variation. This variation is particularly large in the upper 100 m of modified subtropical water and shows the reciprocating influences of the California Current in summer, and of intrusion from the south in winter. The core of the California Current in the northern portion, 330-370 km off San Francisco on CalCOFI line 60, reflects subarctic water, with cool temperatures and low salinities near the surface. Below 100 m the salinity increases rapidly with depth. The effect of mixing with central water is evident farther west, 1,040-1,180 km

seaward from the Southern California Bight along lines 80 and 90. This area reflects the warm temperatures and high salinities of central water in the upper 100 m, with salinities decreasing with depth to a minimum at about 200 m. Equatorial water moving northward along the Baja California coast also mixes into the California Current and is most evident in the southern portion, about 300 km offshore, along lines 133 and 137. Like central water, equatorial water is warm near the surface, but in the layers below 100 m, salinities increase rapidly with depth.

The southern boundary of the subarctic water mass is called the subarctic front. It is found at 40°-43° north, west of 150° west. To the east of that longitude it turns southeast and forms the western boundary of the California Current, where it has been called the California front. The northern boundary of the North Pacific central water is called the subtropical front. It is found at about 31° north, west of 140° west, and also bends southeast at its eastern end. In the transition zone between these fronts is another front, described by Lynn (1986) as the northern subtropical front. At their southern extremes, these fronts become diffuse, and the extension of the California Current turns westward and joins the North Equatorial Current.

It is important to note that the positions of these

boundaries may fluctuate. During the period of this study, in particular, the position of the subarctic front at the North American coastline shifted from 40° north before 1957 to 53° north in 1957–58. Moreover, the waters of the California Current and adjacent zones may contain eddies of tens to hundreds of kilometers in extent. Thus there is a considerable amount of exchange and mixing that must be considered in describing a planktonic fauna in terms of water-mass characteristics and boundaries.

Changes during 1955–60

Long-term annual means in the upper 100 m range from 11° to 18°C for temperature and from 33 to 34 ppt salinity. (Figure 3a, b). The temperature pattern shows the expected warming from north to south and also from inshore to offshore. Salinity increases from north to south and, in the northern part of the pattern, decreases from inshore to offshore out to the core of the California Current. The latter appears as a trough in the salinity field about 330 km from the coast.

A chart of temperature anomaly differences (Figure 3c) reveals that the 1958–59 period was warmer than the 1955–56 period throughout the region. The differences were greatest (exceeding 3°C) in the southern portion and, except for an area south of Punta Eugenia, were greater offshore than inshore. The corresponding chart for salinity anomaly shows that salinities were higher in 1958–59 in the southern portion of the region, with positive differences exceeding 0.4 ppt in the farthest offshore area (Figure 3d). The northern portion, however, had higher salinities in 1955–56 in inshore areas and out to nearly 200 km from the coast.

These charts reflect a northward shift of the contours from 1955–56 to 1958–59, particularly in the temperature field. The displacements of the 12°, 14°, and 16° contours between these periods were approximately 220 km (Figure 4). This shift is reflected by changes of temperature and salinity anomalies along CalCOFI line 100 (off Ensenada, Baja California) during the two periods (Figure 5).

It has been suggested that the lower temperatures in 1955–56 might be associated with stronger northwest winds that would contribute to increased upwelling inshore, and to southward transport offshore in the California Current. We attempted to compare southward transports in the 1955–56 and 1958–59 periods by mapping dynamic height anomalies for the sea surface, relative to 500 m, as a representation of geostrophic flow. The

principal differences between the two periods were found in the values of dynamic height; those representing the 1958–59 period were larger by up to 0.08 dynamic meters over much of the region. However, a comparison of gradients of dynamic height anomalies (as indices of transport) along CalCOFI lines 60 to 110 was inconclusive.

RECURRENT GROUPS

Recurrent group analysis was applied to the entire data set of 192 taxa for the seven-year period from 1954 to 1960 and also to each of the seven years (Figures 6 and 7). From the recurrent group analysis of the composite seven-year set, 30 taxa formed 9 groups (2 groups with 5 taxa each, 2 with 4, 2 with 3, and 3 with 2), and 8 other taxa formed associate relationships with taxa in 1 or more of the 9 groups (Figure 6).² Intergroup affinities formed 2 large complexes, each consisting of 4 recurrent groups, and 1 isolated southern shelf recurrent group (SYNODUS). We refer to these as the northern and southern complexes, since their member taxa had predominately cold- or warm-water distributions, or affinity indices linking them to cold- or warm-water taxa. The SYNODUS group was the primary constituent of a southern shelf complex, which was more fully characterized in analyses of individual years. There were 12 recurrent group members in the northern complex, 14 in the southern complex, and 4 in the isolated SYNODUS recurrent group (Table 1). There were 2 unique associates in the northern complex, 5 unique associates in the southern group, and 1 unique associate in the SYNODUS group. There were 53 affiliated taxa in the northern group, 68 affiliates in the southern complex, and 33 in the SYNODUS recurrent group (Appendix). The significant affinity index between *Engraulis mordax* and *Triphoturus mexicanus* was the only link between the northern and southern complexes.

Northern Complex

In the northern complex the LEUROGLOSSUS group had 5 taxa, CITHARICHTHYS had 3 taxa, and TARLETONBEANIA and SARDINOPS had 2 taxa each (Figure 8). Members of the northern complex over the seven-year period can be found through the survey area in the north-south plane but were more likely to be found nearshore when in the southern reaches. The LEUROGLOSSUS and TARLETONBEANIA groups

²Two additional pairs of taxa formed two isolated groups. One of these, comprising Serranidae and Carangidae, was based on relatively few (43) occurrences; the other, comprising Balistidae and Fistularidae, was formed by a single co-occurrence.

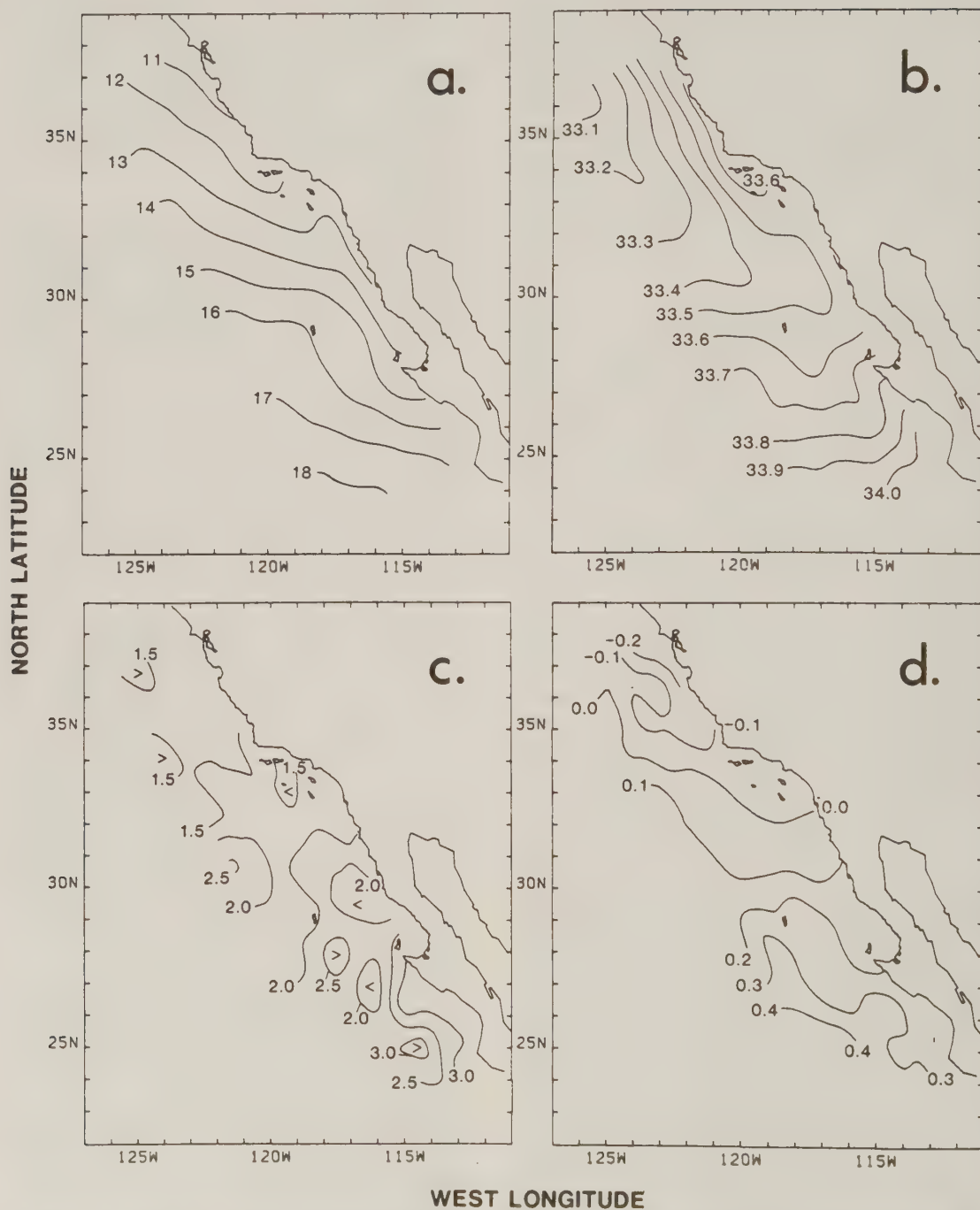


Figure 3. Mean annual temperature (a) and salinity (b) of the upper 100 meters computed at 5 standard depths (10 m, 30 m, 50 m, 75 m, and 100 m) from harmonic coefficients based on data from CalCOFI cruises from 1950 through 1978. Change, or difference, in the deviations of temperatures (c) and salinities (d) in the upper 100 meters from the harmonic means, between the periods 1955-56 and 1958-59.

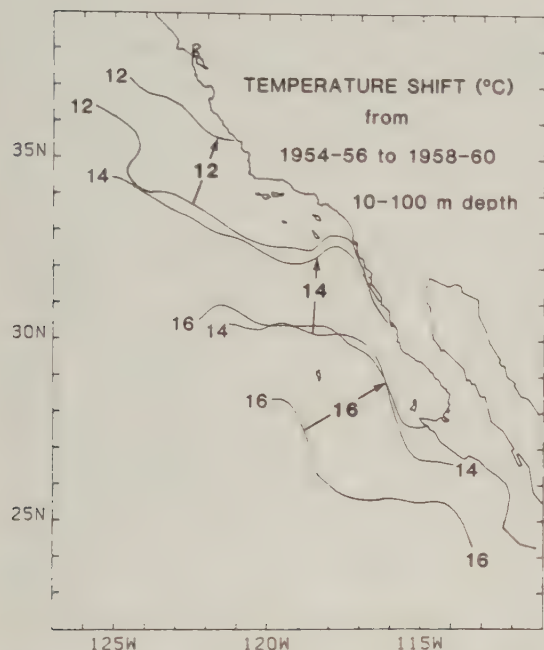


Figure 4. Temperature change in the upper 100 meters between 1955-56 and 1958-59 as depicted by the displacements of the 12°, 14°, and 16°C isotherms between the two periods.

were separated in part by the tendency of the former group to spawn in summer (Table 2). There were significant affinities between *Tarletonbeania crenularis* and 3 of the 5 members of the LEUROGLOSSUS group. Although the distribution of the

TARLETONBEANIA group leads one to believe that it was somewhat more northerly than the LEUROGLOSSUS group, this may be because the cruises proceeded farther north in summer, when this group was spawning.

LEUROGLOSSUS recurrent group. This group is made up of 2 mesopelagic argentinoid smelts (*Bathylagus ochotensis* and *Leuroglossus stilbius*), a vertically migrating mesopelagic myctophid (*Stenobrachius leucopsarus*), a schooling gadoid (*Merluccius productus*), and the scorpaenid genus (*Sebastes* spp.), which includes about 60 species in the survey area (Table 2). Faunal associations of the 4 species are subarctic-transitional or transitional; their spawning is highly seasonal, with winter or spring maxima (Table 2). The fifth taxon, the rockfishes of the genus *Sebastes*, is broadly distributed from boreal to transitional waters and has a composite fall-to-spring spawning season with a February peak in the survey area (Table 2).

The distribution for the LEUROGLOSSUS group in the survey area was centered in the Southern California Bight region (Figure 9), reflecting the geographic distribution of *L. stilbius* larvae (Table 3). Populations of *B. ochotensis* and *S. leucopsarus* have more northerly distributions, extending across the subarctic Pacific; their larvae were found predominately in the northern part of the survey pattern, off northern and central California (Table 3). Larvae of *L. stilbius* and *S. leucopsarus* have a more shoreward distribution than *B. ochotensis* larvae. Adults of *M. productus* have a broad distribution from the boreal region to Baja

TABLE 1

Numbers of Larval Fish Taxa That Are Members, Associates, or Affiliates of Recurrent Groups in an Analysis of Pooled Data from CalCOFI Surveys, 1954-60

Complex	Group name	Members	Associates	Unique associates	Affiliates
Northern	LEUROGLOSSUS	5	4	0	19
	CITHARICHTHYS	3	7	1	21
	SARDINOPS	2	3	0	5
	TARLETONBEANIA	2	3	0	8
	Subtotal	12	*	1	53
Southern	SYMBOLOPHORUS	5	7	1	16
	VINCIGUERRIA	4	6	2	32
	TRIPHOTURUS	3	10	0	9
	CERATOSCOPELUS	2	4	0	10
	Subtotal	14	*	3	66
Southern shelf	SYNODUS	4	0	1	32
Total		30	*	5	151

*Not unique sets

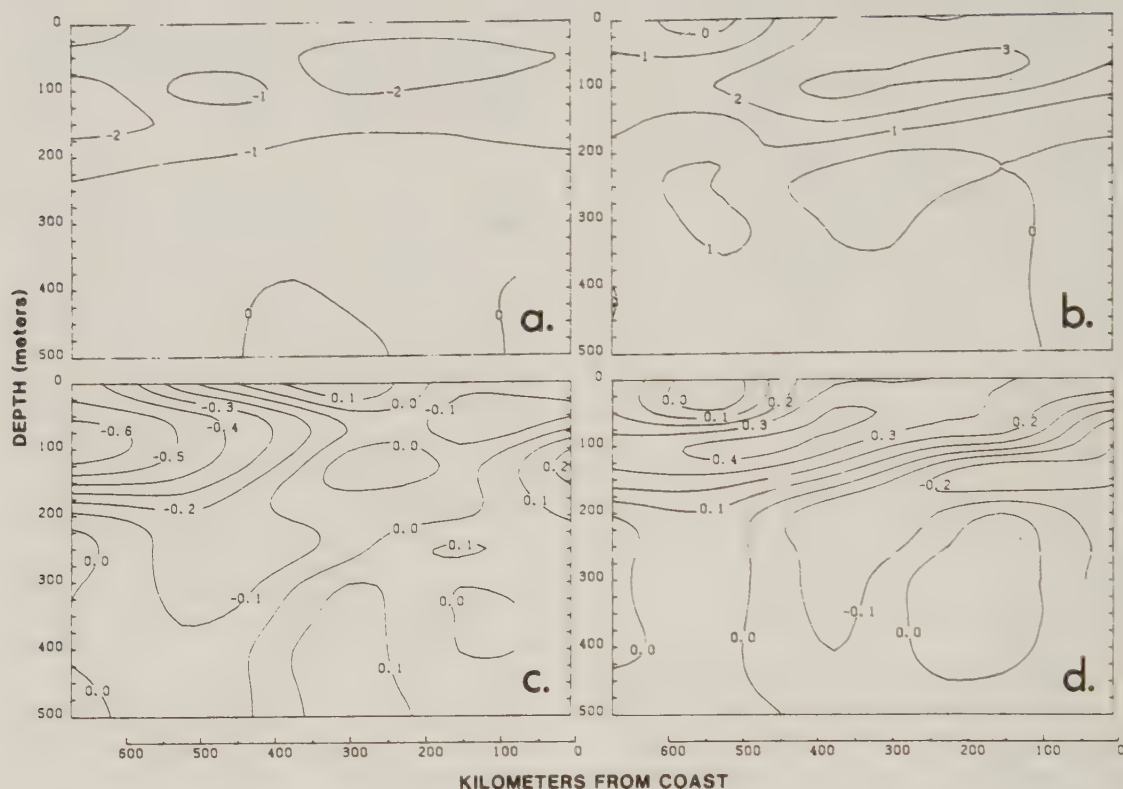


Figure 5. Mean temperature anomaly pattern along CalCOFI line 100 in the upper 500 meters, 1955-56 (a), and 1958-59 (b). Mean salinity anomaly pattern (computed in the same way) for 1955-56 (c) and 1958-59 (d). The isopleths represent deviations from harmonic means based on the period 1950-78.

California, with a postulated migration to spawning grounds off southern California and northern Baja California. The high mean abundance off southern Baja California may represent a few anomalously large collections in winter (Table 3). Larvae of *Sebastes* spp. were concentrated in the shoreward regions off California and northern Baja California.

The LEUROGLOSSUS group was strongly connected with other groups of the northern complex. Four of the group taxa had strong affinities with *Engraulis mordax*; 3 had affinities with *Sardinops sagax*; and 3 had affinities with *Tarletonbeania crenularis* (Figures 6 and 8).

TARLETONBEANIA recurrent group. This group comprises a vertically migrating mesopelagic myctophid (*Tarletonbeania crenularis*) and an epipelagic oceanic stromateoid (*Icichthys lockingtoni*). Adults of *T. crenularis* range from British

Columbia to central Baja California. The range for *I. lockingtoni* is similar in the south, but extends westward to the Gulf of Alaska and Japan. These two species have well-defined spawning seasonality, with summer maxima (Table 2).

The distribution of the group was coincident with the LEUROGLOSSUS group (Figure 9), and members of the 2 groups would have higher affinity indices if the spawning seasons were coincident. Larval distributions for the 2 species in the TARLETONBEANIA groups were concentrated heavily in northern and central California, with a strong peak in northern California for larvae of *T. crenularis* (Table 3).

CITHARICHTHYS recurrent group. This group comprises a coastal pelagic anchovy (*Engraulis mordax*) and 2 shallow-water paralichthyid flatfishes (*Citharichthys fragilis* and *C. xanthostigma*). *E. mordax* has a broad coastal distribution from

TABLE 2
Taxonomic Composition of Recurrent Groups, Number of Observations (1954-60) and Distribution and Spawning
Seasons of Members

Recurrent group taxa	Number	Faunal association	Adult habitat	Spawning season /peak month
Northern Complex				
LEUROGLOSSUS group				
<i>Bathylagus ochotensis</i>	1172	S-T	MP (49-901 m)	Win-Spr/May
<i>Leuroglossus stilbius</i>	3011	T	MP (to 690 m)	Spr/Mar
<i>Stenobranchius leucopsarus</i>	2440	S-T	MP (MEP)	Spr/Feb-May
<i>Sebastes</i> spp.	4486	S-T,T	D (to 732 m)	Fall-Spr/Feb-Mar
<i>Merluccius productus</i>	3027	S-T	D (to 914 m)	Win-Spr/Feb-Mar
TARLETONBEANIA group				
<i>Tarletonbeania crenularis</i>	1044	S-T	MP (MEP)	Spr-Sum/May-Jul
<i>Ichthyos lockingtoni</i>	634	S-T	EP (to 91 + m)	Sum/Jun-Jul
CITHARICHTHYS group				
<i>Engraulis mordax</i>	5098	T	CP (to 219 m)	Ext/Feb-Mar
<i>Citharichthys fragilis</i>	819	T,SbTr	D (18-347 m)	Bim/Aug, Feb
<i>Citharichthys xanthostigma</i>	980	TtoTr	D (2-200 m)	Bim/Aug, Feb
SARDINOPS group				
<i>Sardinops sagax</i>	1479	T	CP	Ext/Jan-Mar, Aug-Sep
<i>Scomber japonicus</i>	513	T,SbTr	CP	Sum/Aug
Southern Complex				
SYMBOLOPHORUS group				
<i>Bathylagus wesethi</i>	1913	T	MP (40-1,001 m)	Spr-Sum/May
<i>Cyclothone</i> spp.	1784	WWC	MP	Sum-Fall/Aug
<i>Diogenichthys atlanticus</i>	734	WWC	MP (MEP)	Bim/May, Sep-Oct
<i>Lampanyctus ritteri</i>	2288	S-T	MP (MEP)	Spr/May
<i>Symbolophorus californiensis</i>	966	T	MP (MEP)	Spr/May
TRIPHOTURUS group				
<i>Triphoturus mexicanus</i>	4648	SbTr	MP (MEP)	Sum/Aug
<i>Protomyctophum crockeri</i>	2303	T	MP	Spr/May
<i>Trachurus symmetricus</i>	2096	T	EP (to 183 m)	Spr-Sum/May, Jun
CERATOSCOPELUS group				
<i>Ceratosphepus townsendi</i>	988	T	MP (MEP)	Sum/Aug
<i>Lampadena urophasos</i>	307	SbTr	MP (MEP)	Sum/Aug
VINCIGUERRIA group				
<i>Vinciguerria lucetia</i>	4288	ETP	MP (MEP)	Ext/Aug
<i>Diogenichthys laternatus</i>	2203	ETP	MP (MEP)	Ext/Jan-Feb, Aug-Oct
<i>Gonichthys tenuiculus</i>	537	ETP	MP (MEP)	Ext/Feb
<i>Hygophum atratum</i>	444	ETP	MP (MEP)	Bim/Jan, Aug
Southern Coastal Complex				
SYNODUS group				
<i>Synodus</i> spp.	402	SbTr, Tr	D (to 50 m)	Fall/Sep-Dec
<i>Prionotus</i> spp.	132	SbTr, Tr	D (15-110 m)	Sum-Fall/Aug-Sep
<i>Ophiodon scrippsae</i>	192	T, SbTr	D (3-70 m)	Sum-Fall/Aug-Sep
<i>Symphurus</i> spp.	351	T, Tr	D (1-201 m)	Sum-Fall/Aug-Sep

Abbreviations:

S = subarctic, T = transition, SbTr = subtropical, Tr = tropical, WWC = warm-water cosmopolite, ETP = eastern tropical Pacific, MP = mesopelagic, MEP = migrates to epipelagic, EP = epipelagic, D = demersal, CP = coastal pelagic, Bim = bimodal, Ext = extended.

Information on the distribution of adult fishes summarized from Miller and Lea (1972), Eschmeyer et al. (1983), Wisner (1976), and original data

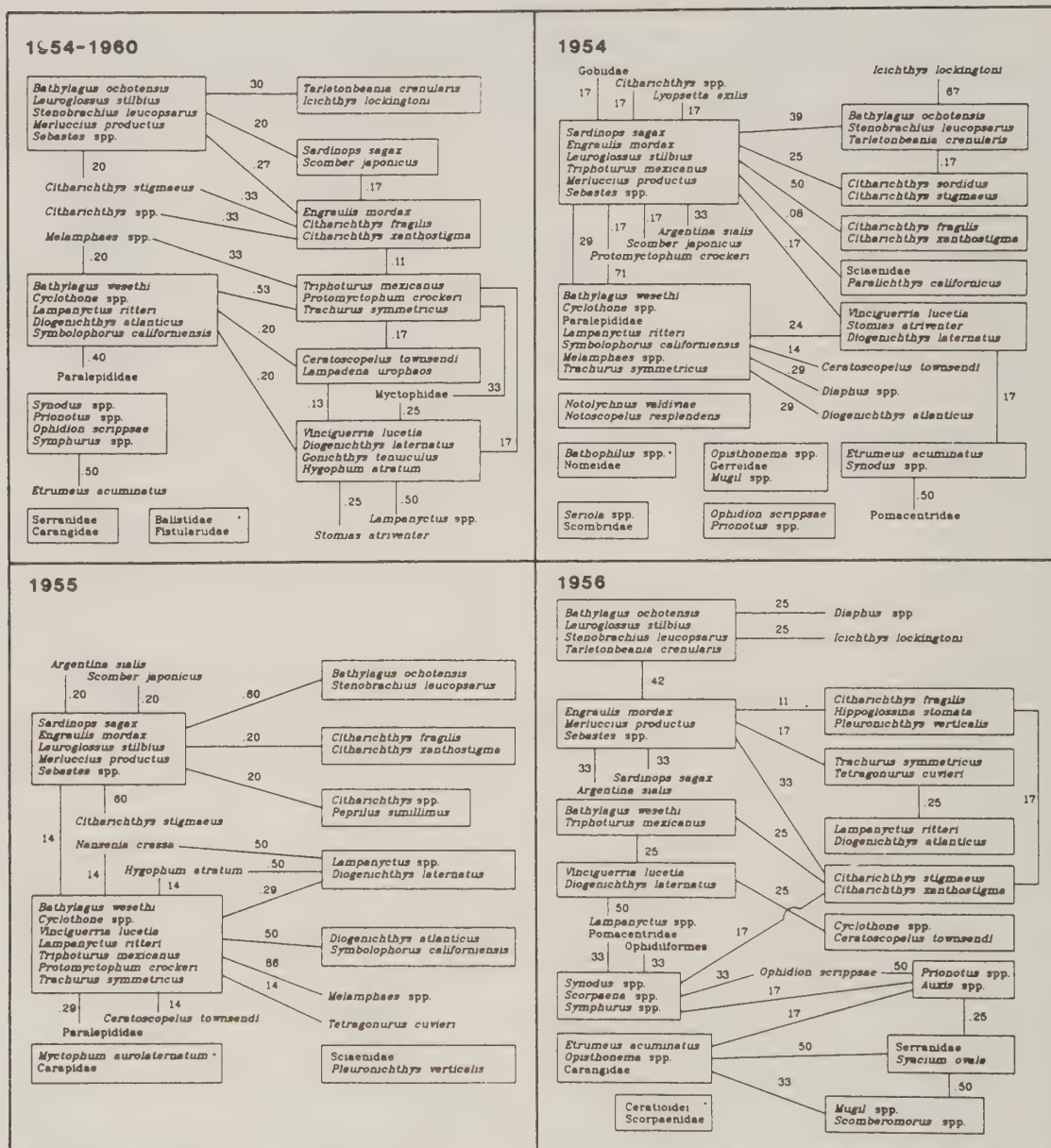


Figure 6. The composition and interrelationships of recurrent groups and their associates in the CalCOFI survey area for pooled 1954-60 data and for three individual years. A line between two recurrent groups indicates that there are intergroup pairs with significant affinity indices (≥ 0.3). The number represents the fraction of significant affinity pairs divided by the possible number of pairs. Recurrent groups represented by a single co-occurrence are indicated by an asterisk.

British Columbia to southern Baja California; however, there are apparently three subpopulations—a northern population extending from cen-

tral California northward, a central population distributed from central California to central Baja California, and a southern stock from central Baja

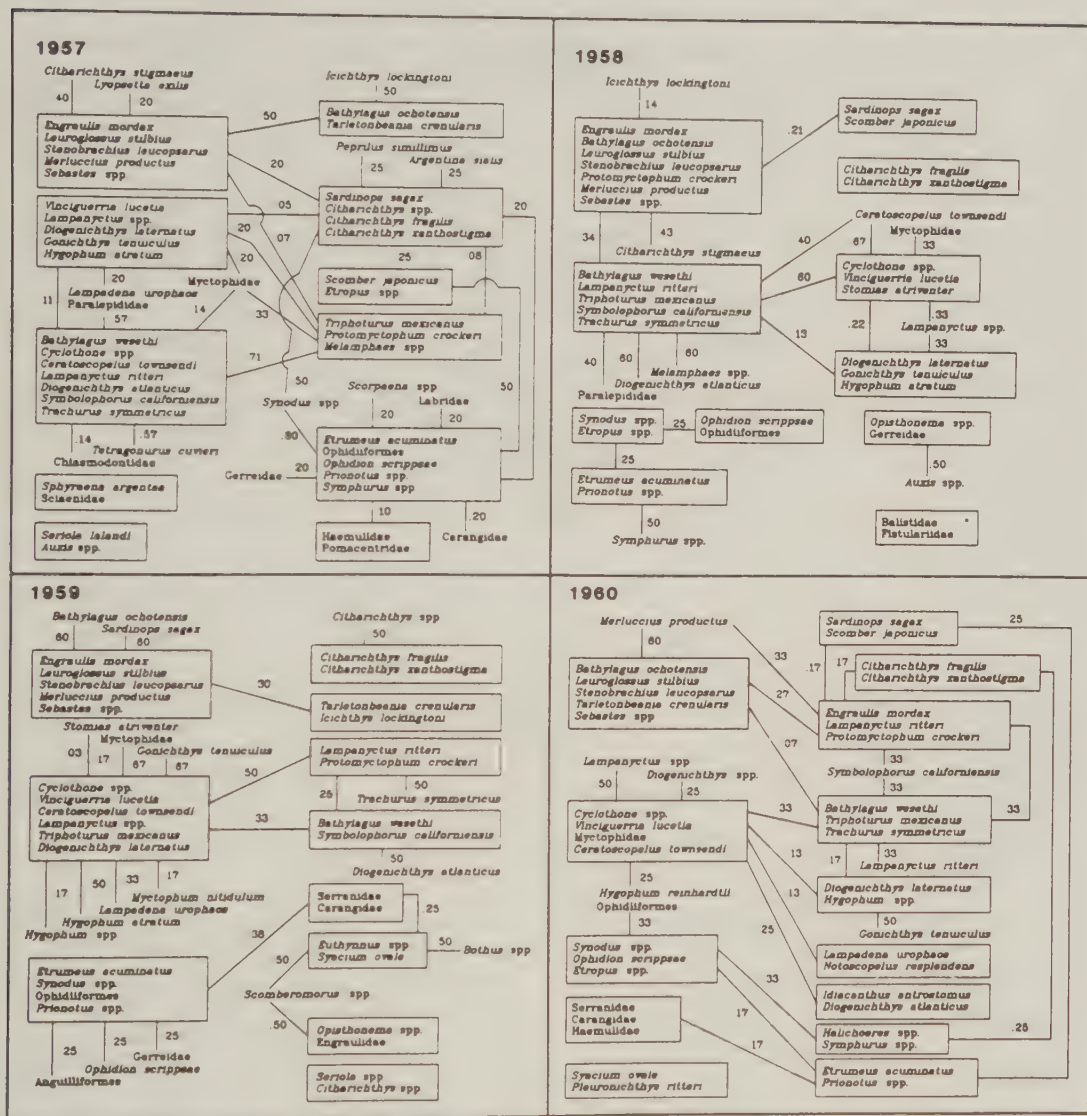


Figure 7. The composition and interrelationships of recurrent groups and their associates in the CalCOFI survey for 1957-60. A line between two recurrent groups indicates that there are intergroup pairs with significant affinity indices (≥ 0.3). The number represents the fraction of significant affinity pairs divided by the possible number of pairs. Recurrent groups represented by a single co-occurrence are indicated by an asterisk.

California to Cabo San Lucas. The 2 flatfishes have warm-water faunal affinities, with ranges extending from southern California south to the Gulf of California, and were included in the northern complex because of their strong affinity indices with *E. mordax*. Two other flatfish taxa form associate relationships with *E. mordax*—the genus *Citharichthys* as a unique associate and *Citharichthys stig-*

maeus as an associate shared with *Sebastes* spp. in the LEUROGLOSSUS group³. *C. stigmaeus* is more temperate than its group congeners, with a range extending from Alaska to southern Baja California. A third associate relationship is with the

³The category *Citharichthys* spp. consists of small, damaged specimens of the four common species of this genus present in the CalCOFI region, and is of limited significance in this analysis

TABLE 3
Geographic Distribution (Percent of Total Abundance) of Recurrent Group Larval Fish Taxa in Eleven Areas of the CalCOFI Sampling Pattern, 1954-60

Taxon	CCal		SCal		NBCal			CBCal		SBCal	
	In	Off	In	Off	In	SVB	Off	In	Off	In	Off
Northern Complex											
LEUROGLOSSUS group											
<i>Bathylagus ochotensis</i>	17	43	8	25	2	1	4	T	0	0	0
<i>Leuroglossus stilbius</i>	12	6	38	22	5	3	5	4	4	T	T
<i>Stenobranchius leucopsarus</i>	20	32	22	24	1	0	2	T	0	0	0
<i>Sebastes</i> spp.	27	7	32	10	6	7	2	5	2	1	T
<i>Merluccius productus</i>	6	11	8	26	6	4	15	4	2	19	T
TARLETONBEANIA group											
<i>Tarletonbeania crenularis</i>	22	57	3	17	T	T	T	0	0	0	0
<i>Ichthyos lockingtoni</i>	19	48	3	26	T	T	3	T	T	T	0
CITHARICHTHYS group											
<i>Engraulis mordax</i>	4	2	26	7	9	17	5	17	7	6	T
<i>Citharichthys fragilis</i>	0	0	T	0	2	68	1	17	10	1	T
<i>Citharichthys xanthostigma</i>	T	0	T	T	2	38	4	29	22	2	T
SARDINOPS group											
<i>Sardinops sagax</i>	T	T	10	6	3	24	9	21	4	21	1
<i>Scomber japonicus</i>	0	T	6	3	3	30	9	14	4	29	2
Southern Complex											
SYMBOLOPHORUS group											
<i>Bathylagus wesethi</i>	T	3	T	22	3	3	47	1	18	T	2
<i>Cyclothone</i> spp.	T	1	T	12	T	T	43	2	39	T	T
<i>Diogenichthys atlanticus</i>	T	10	1	27	2	1	44	T	13	0	0
<i>Lampanyctus ritteri</i>	3	16	2	26	2	2	32	T	15	T	1
<i>Symbolophorus californiensis</i>	1	11	1	31	3	1	44	T	6	0	0
TRIPHOTURUS group											
<i>Triphoturus mexicanus</i>	T	T	1	5	5	5	32	7	41	T	3
<i>Protomyctophum crockeri</i>	4	21	3	25	3	2	26	2	13	0	T
<i>Trachurus symmetricus</i>	7	16	2	41	2	1	27	T	4	0	T
CERATOSCOPELUS group											
<i>Ceratospheus townsendi</i>	T	2	T	7	T	T	45	T	42	T	2
<i>Lampadena urophas</i>	0	0	0	5	T	1	38	5	45	T	4
VINCIGUERRIA group											
<i>Vinciguerria lucetia</i>	T	T	T	4	T	T	24	2	38	6	26
<i>Diogenichthys lateratus</i>	0	0	T	T	T	T	7	6	36	12	38
<i>Gonichthys tenuiculus</i>	0	0	T	T	T	T	10	4	42	10	33
<i>Hygophum atratum</i>	0	0	0	0	T	T	3	2	23	11	61
Southern Coastal Complex											
SYNODUS group											
<i>Synodus</i> spp.	0	0	T	0	2	30	T	32	2	32	2
<i>Prionotus</i> spp.	0	0	0	0	0	1	0	64	T	20	T
<i>Ophiodon scrippsae</i>	1	T	3	T	T	28	T	42	6	16	T
<i>Symphurus</i> spp.	T	0	3	T	T	23	3	28	24	4	13

Abbreviations:

CCal = Central California (CalCOFI lines 60-77)
SCal = Southern California (CalCOFI lines 80-97)
NBCal = Northern Baja California (CalCOFI lines 100-117)
CBCal = Central Baja California (CalCOFI lines 120-137)
SBCal = Southern Baja California (CalCOFI lines 140-157)

In = Inshore portion of section (usually less than 100 km)

Off = Offshore portion of section (about 100-400 km)

SVB = Bahía Sebastián Viscaíno

T = Trace amounts of larvae (less than 0.5%)

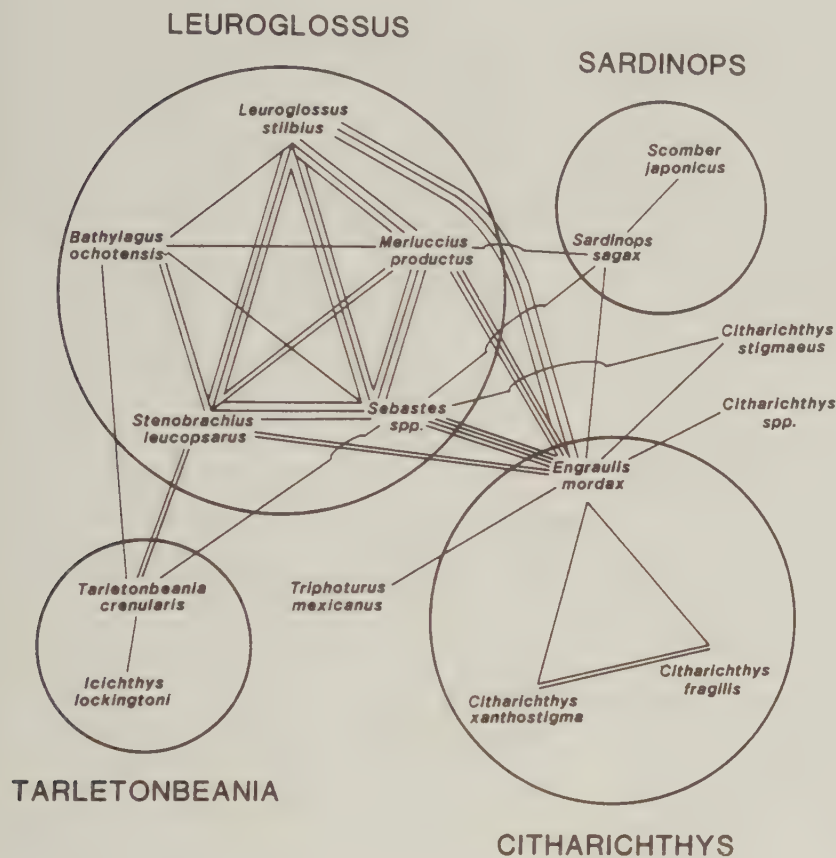


Figure 8. The northern complex of recurrent groups and associates from pooled (1954-60) CalCOFI data. The number of connecting lines indicates the approximate affinity index value. A single line represents an affinity index from 0.30 to 0.39; a double line is 0.40 to 0.49; a triple line is 0.50 to 0.59; and four lines represent an affinity index of 0.60 or greater.

myctophid *Triphoturus mexicanus* in the southern complex. *Engraulis mordax* has a protracted spawning season with a February-March maximum, and the 2 species of *Citharichthys* in the group have bimodal spawning seasons with February and August peaks (Table 3).

The group distribution was centered off coastal northern and central Baja California (Figure 9). Larvae of *E. mordax* were broadly distributed along the coast of the entire survey area, with highest abundance from southern California to central Baja California. Larvae of the two *Citharichthys* species were essentially confined to Baja California, with peak abundance in Bahía Sebastián Viscaíno and the adjoining region to the south.

SARDINOPS recurrent group. The group comprises 2 coastal pelagic species—a clupeid (*Sardinops sagax*) and a scombrid (*Scomber japonicus*).

The Pacific sardine, *S. sagax*, is primarily distributed off California and Baja California and in the Gulf of California. In the southern hemisphere another subspecies occurs off Chile and Peru. The chub mackerel, *S. japonicus*, has a worldwide distribution in temperate and tropical waters, particularly in boundary-current regions. *S. sagax* formed associate relationships with *Sebastes* spp. and *M. productus* in the LEUROGLOSSUS group and with *E. mordax* in the CITHARICHTHYS group. *S. sagax* has a protracted, almost year-round spawning season, with apparent peaks in late winter and late summer; *S. japonicus* has a restricted summer spawning season (Table 3).

The SARDINOPS group has a broad coastal distribution from Point Conception, California, to Cabo San Lucas, Baja California (Figure 9). Larvae of the two species had their highest mean abundance in Bahía Sebastián Viscaíno and along the coast south to Cabo San Lucas (Table 3).

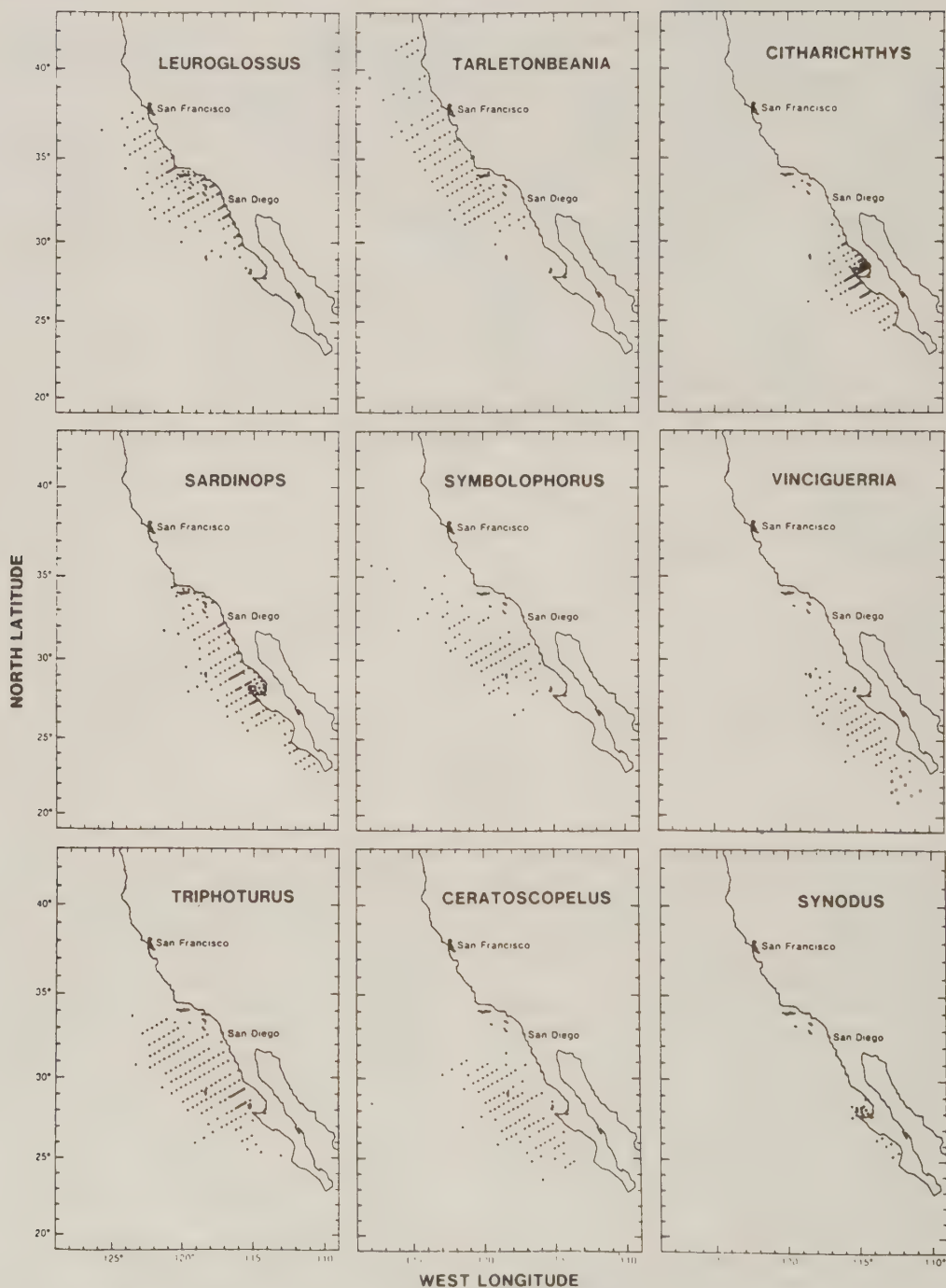


Figure 9. Geographic distribution of recurrent groups of larval fishes in the CalCOFI survey area. The general area for each recurrent group has been approximated by the dots, which represent station positions in which at least one sample in seven years (1954-60) had all recurrent group members present.

Southern Complex

The southern complex was made up of 4 recurrent groups: SYMBOLOPHORUS, TRIPHOTURUS, VINCIGUERRIA, and CERATOSCOPELUS (Figure 10). As in the northern complex, the largest group was connected by shared associates in all the other groups. SYMBOLOPHORUS had 5 member taxa, 7 associates in other recurrent groups, and 1 unique associate. VINCIGUERRIA had 4 member taxa, 6 associates in other recurrent groups, and 2 unique associates. TRIPHOTURUS had 3 member taxa, 8 associates in other groups, and 2 unique associates. CERATOSCOPELUS had 2 members, 4 associates in other groups, and no unique associates.

SYMBOLOPHORUS recurrent group. The group comprises 5 mesopelagic taxa—an argentinoid smelt (*Bathylagus wesethi*), 3 vertically migrating myctophids (*Diogenichthys atlanticus*, *Symbolophorus californiensis*, *Lampanyctus ritteri*), and the stomiiform genus *Cyclothone* (Table 2). *B. wesethi* and *S. californiensis* are transitional species characteristic of the California Current region, with distributions extending from the subarctic boundary to central Baja California. *L. ritteri* has a broader subarctic-transitional distribution that includes the Gulf of Alaska. *D. atlanticus* is a warm-water cosmopolite that enters the California Current region off southern California and northern Baja California. Seven species of *Cyclothone* are known from the California Current region. Adult samples are dominated by 2 species, *C. signata* and *C. acclinidens*, and preliminary identifications indicate that this is also true for ichthyoplankton samples. Both species have primarily equatorial distributions in the Pacific; these extend northeastward into the California Current region. Members of the SYMBOLOPHORUS group express a strong spawning seasonality, with *B. wesethi*, *L. ritteri*, and *S. californiensis* peaking in May and *Cyclothone* in August. *D. atlanticus* is bimodal, with peaks in May and September-October.

Group members form a strong affinity network with all other recurrent groups in the southern complex, which includes 7 groups and 2 individual associates (Figure 10). *L. ritteri* and *B. wesethi* were associates of the mesopelagic genus *Melamphaes*, which was also associated with *Trachurus symmetricus* in the TRIPHOTURUS group. Two species are common in the California Current region: *M. parvus*, which is restricted to this region, and *M. lugubris*, a subarctic-transitional form that ranges westward across the North Pacific.

Spawning in *Melamphaes* is highly seasonal, with a peak in May. Paralepididae, a family of mesopelagic predators, was an associate with *B. wesethi*. One paralepidid species, *Lestidiops ringens*, predominates in the adult and larval samples from the California Current region.

The SYMBOLOPHORUS group had an offshore distribution in the central portion of the survey area, impinging on the coast of northern Baja California (Figure 9). Except for *L. ritteri*, all species had their highest larval abundances in the southern California-northern Baja California offshore region (Table 3). *L. ritteri* larvae were slightly more abundant in the northern Baja California offshore region (Table 3).

VINCIGUERRIA recurrent group. This group comprises 4 mesopelagic vertical migrators—the stomiiform lightfish *Vinciguerria lucetia* and 3 myctophine lanternfishes, *Diogenichthys laternatus*, *Gonichthys tenuiculus*, and *Hygophum atratum* (Table 2). All are eastern tropical Pacific species that range northward to the Gulf of California and the outer coast of Baja California. All have extended spawning seasons: *V. lucetia* peaks in August; *D. laternatus* and *H. atratum* have winter and summer maxima; and *G. tenuiculus* peaks in February (Table 2).

Group members form a strong affinity network with all other groups in the southern complex, including 5 group associates and 3 individual associates (Figure 10). *V. lucetia* and *D. laternatus* are associates of the myctophid genus *Lampanyctus*, which includes at least a dozen species from the California Current region; the unidentified Myctophidae is an associate shared with *T. mexicanus* of the TRIPHOTURUS group. Unidentified larval Myctophidae in our collections are either small or disintegrated specimens that represent a spectrum of the 40 or more species reported from this region. *Stomias atriventer*, a mesopelagic predator, is a unique associate of *V. lucetia*. *S. atriventer* is found from central California to mid-Mexico and has an extended spawning season with a winter-spring maximum.

The VINCIGUERRIA group is distributed principally in the offshore central Baja California and inshore-offshore southern Baja California regions (Figure 9). Only *V. lucetia* occurs in appreciable numbers in offshore northern Baja California waters (Table 3).

TRIPHOTURUS recurrent group. This group comprises 2 mesopelagic lanternfishes (*Protomyctophum crockeri* and *Triphoturus mexicanus*) and

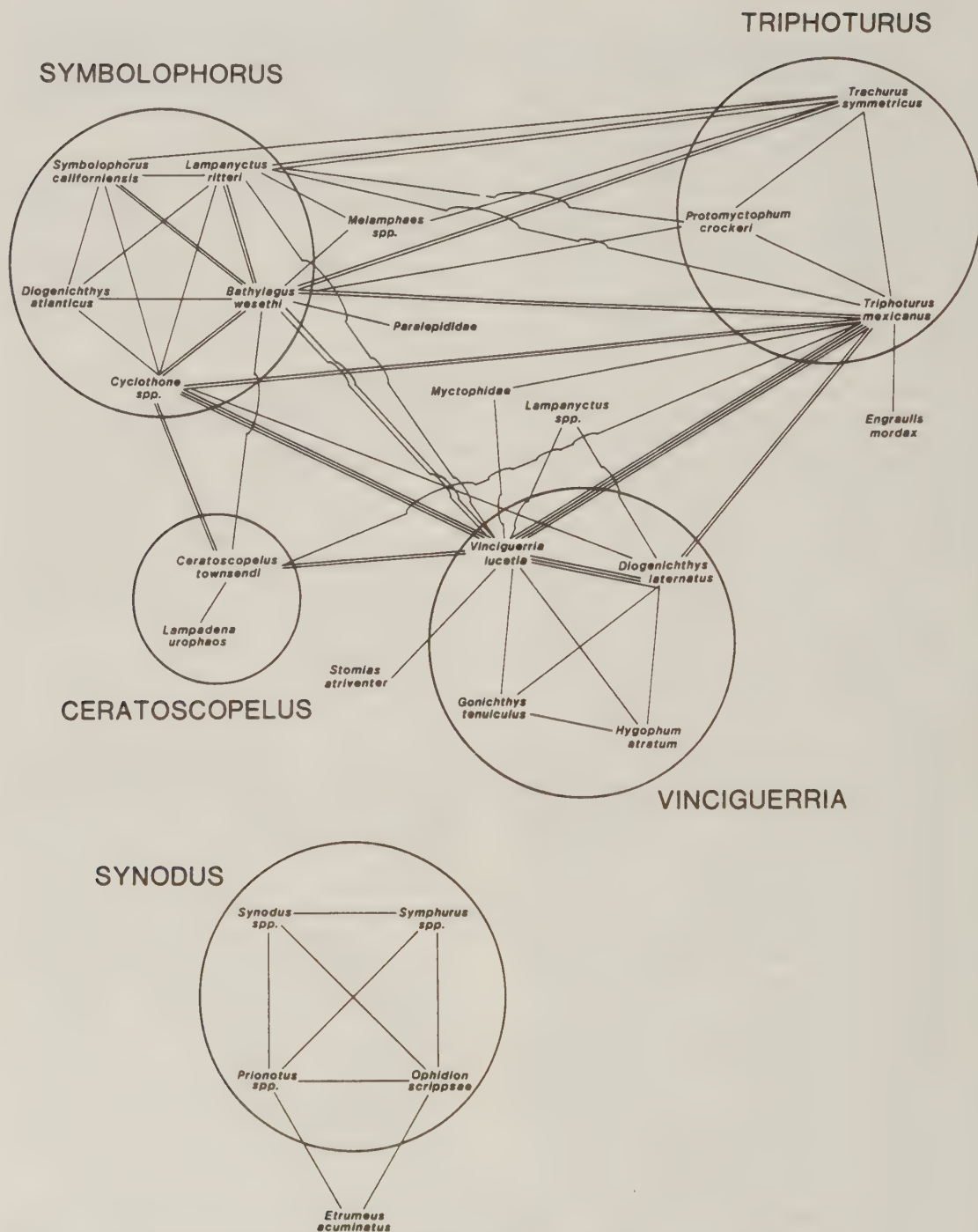


Figure 10. The southern complex and southern coastal complex of recurrent groups and associates from pooled (1954-60) CalCOFI data.

an epipelagic carangid (*Trachurus symmetricus*). *P. crockeri* is a transitional species ranging from central Baja California northward to the coast of Washington and westward to Japan. *T. mexicanus* occurs between 38° and 20°N in the California Current region and in the Gulf of California, with disjunct populations across the tropics (Hulley 1986). The jack mackerel, *T. symmetricus*, occurs from the Gulf of Alaska southward to Cabo San Lucas, Baja California, and has a principal distribution from southern California to central Baja California. Older year classes are noted for their offshore distribution, which can extend 2,400 kilometers seaward. *P. crockeri* has a bimodal spawning pattern with peaks in May and November; *T. mexicanus* peaks in August; and *T. symmetricus* in May-June (Table 2).

The TRIPHOTURUS group was strongly connected with the 2 larger recurrent groups of the southern complex and weakly connected to the CERATOSCOPELUS group (Figure 10). Associations were formed with 7 members of these groups and with 2 individual taxa. The association between *T. mexicanus* and *E. mordax* linked the northern and southern complexes (Figures 6 and 10).

The group had a broad inshore-offshore distribution in the survey area, extending from central California to central Baja California; this reflected the broad distributions of larvae of these species (Figure 9; Table 3).

CERATOSCOPELUS recurrent group. This group comprises 2 vertically migrating myctophids, *Ceratoscopelus townsendi* and *Lampadena urophaos*. *C. townsendi* is a resident of the California Current region, between 45° and 20°N latitude; *L. urophaos* has a more subtropical distribution that extends westward to Hawaii. Both are highly seasonal spawners, with summer maxima (Table 2).

Affinities exist with all other groups in the southern complex, although only weakly with TRIPHOTURUS (Figure 10). The group's distribution was centered off northern and central Baja California and distinctly offshore, reflecting the areal abundance patterns of both species (Figure 9; Table 3).

Southern Shelf Complex

Four shallow demersal taxa from 4 separate orders form the SYNODUS group—the myctophiform genus *Synodus*, the scorpaeniform genus *Prionotus*, the pleuronectiform genus *Symphurus*, and the ophiidiiform species, *Ophiodon scrippsae* (Figure 6). In our survey area adult collections of the 3 generic taxa are dominated by 3 species: *Syn-*

odus lucioceps, *Prionotus stephanophrys*, and *Symphurus atricauda*. *S. lucioceps* and *O. scrippsae* are temperate-subtropical species ranging from central California to the Gulf of California. *P. stephanophrys* has a broad distribution that extends from the Columbia River (rarely north of Mexico) to Chile, and *S. atricauda* ranges from Oregon (rarely north of southern California) to Panama. The taxa have well-defined summer-fall spawning seasons, peaking in August-September. Spawning in *Synodus* spp. appears to be bimodal, with peaks in September and December (Table 2).

Although this group borders on all groups of the southern complex, no associate affinities were formed with any other recurrent group; the group had one unique associate, *Etrumeus acuminatus*, a coastal pelagic clupeid (Figure 6). This species ranges from central California to Chile and spawns during the summer.

Coincident samples for this group were found only in the widest continental shelf region in the survey area. Bahía Sebastián Viscaíno and southerly along the Punta Abreojos-Cabo San Lázaro Bight (Figure 9). Mean larval abundances were high in both these regions, except for *Prionotus*, which had a low abundance in Bahía Sebastián Viscaíno (Table 3).

The application of the REGROUP procedure to the combined 1954-60 data set at three higher affinity levels (0.4, 0.5, 0.6) provided a hierarchical view of the relationships of the principal larval fish taxa. At a critical level of 0.4, two large groups representing the northern and southern complexes were formed. The northern group included *E. mordax*, *L. stilbius*, *S. leucopsarus*, *M. productus*, and *Sebastes* spp., with *B. ochotensis* as an associate. The southern group consisted of *B. wesethi*, *Cyclothone* spp., *V. lucetia*, and *T. mexicanus*, with *C. townsendi*, *D. laternatus*, and *S. californiensis* as associates. This group was linked to a group pair, *L. ritleri*-*T. symmetricus*, by 3 out of 8 possible intergroup pairings. *Citharichthys fragilis* and *C. xanthostigma* formed an isolated group pair.

At a critical affinity index value of 0.5, the groups were reduced and fragmented. The northern complex consisted of 2 small groups—*E. mordax*-*L. stilbius*-*M. productus* and *S. leucopsarus*-*Sebastes* spp.—linked by 4 of 6 possible intergroup pairings. The southern complex was represented by a group pair—*V. lucetia*-*T. mexicanus*—with *Cyclothone* spp. and *D. laternatus* as associates. At a critical level of 0.6 only 2 group pairs remained: *E. mordax*-*Sebastes* spp. and *V. lucetia*-*T. mexi-*

canus, representing the northern and southern complexes, respectively.

INTERANNUAL VARIATION IN RECURRENT GROUPS

A total of 76 taxa were either group members or associates during the individual years over the seven-year period (Figures 6 and 7). The numbers of recurrent groups ranged from 8 in 1955 to 14 in 1956 and 1960. Number of taxa per group ranged from 2-4 in 1956 to 2-7 in 1954, 1955, 1957, and 1958. The average number of taxa per group was lowest in 1955 (2.4 taxa/group) and highest in 1957 (3.5/group). The total number of taxa contributing to recurrent groups ranged from 24 in 1955 to 39 in 1957. Associate taxa ranged from 8 in 1956 and 1960 to 14 in 1957. There were 2 shared associate taxa (those which form associate links with 2 or more groups) in 1957 and 1 in each of the other years.

There was considerable rearrangement of recurrent groups and group components during the seven-year period; however, the northern and southern complexes, as described in the preceding analysis of the composite seven-year data set, were generally conserved (Figures 6 and 7). In four of the years, group members of one complex became group members of another complex. In 1954 the southern complex species, *Triphoturus mexicanus*, formed a group with 5 northern complex taxa, and in 1958 another southern complex species, *Proto-myctophum crockeri*, combined with a similar group of 6 northern taxa. In 1960, *Engraulis mordax* formed a group with 2 southern complex species, *P. crockeri* and *Lampanyctus ritteri*. In 1957 the northern complex and southern coastal complexes were linked by the recurrent group pairing of *Scomber japonicus* and the paralichthyid flatfish, *Etropus* spp. (Figures 6 and 7).

The complexes were also linked when significant affinity indices were formed between northern and southern taxa. In 1954 the high proportion (0.29) of associate linkages between the largest northern and southern groups resulted from the inclusion of *T. mexicanus* in the northern group (Figure 6). This species was an associate of all taxa except Paralichthyidae in the 7-member southern group. Other pairs contributing to this intergroup connection were *Sebastes* spp.-*T. symmetricus*, *M. productus*-*T. symmetricus*, *B. wesethi*-*M. productus*, *S. sagax*-*L. ritteri*, and *S. sagax*-*T. symmetricus*. The inclusion of *T. mexicanus* in the northern group was also responsible for the other northern-southern link-

ages, since it was an associate of *P. crockeri* and formed associate relationships with each member of the group formed by *V. lucetia*, *S. atriventer*, and *D. laternatus* (Figure 6). In 1955, *T. symmetricus* in the 7-member southern group was largely responsible for the north-south linkage, since it formed associate relationships with *S. sagax*, *L. stilbius*, and *Sebastes* spp. of the 5-member northern group. The northern species *L. stilbius* also formed associations with *T. mexicanus* and *P. crockeri* of the southern group (Figure 6).

In 1956 the northern-southern connections were keyed to the group formed by the sanddabs *C. stig-maeus* and *C. xanthostigma*, and also involved the southern coastal complex. The two species formed associate relationships with *T. mexicanus* in the *T. mexicanus*-*B. wesethi* group and with *Symphurus* spp. in the 3-member southern coastal group. Another northern-southern linkage was between *T. symmetricus* of the *T. symmetricus*-*Tetragonurus cuvieri* group and *M. productus* of the *E. mordax*-*M. productus*-*Sebastes* spp. group (Figure 6).

In 1957, northern-southern linkages also involved a group predominated by sanddab taxa (*Citharichthys* spp.-*C. fragilis*-*C. xanthostigma*-*S. sagax*) and a 5-member southern coastal group (Figure 7). *Symphurus* spp. of the latter group formed associate ties with all but *C. fragilis* in the northern group, and *O. scrippsae* of the southern group was an associate of *Citharichthys* spp. The shared associate, *Synodus* spp., further linked the two groups; it had significant affinities with all but *E. acuminatus* in the southern coastal group and also with *S. sagax* and *C. xanthostigma* in the northern group. The intercomplex group formed by *Scomber japonicus* and *Etropus* spp. was strongly linked with the large southern coastal group; *S. japonicus* was an associate of *E. acuminatus*, *O. scrippsae*, and *Symphurus* spp.; *Etropus* spp. had associate ties with the latter two. The *S. japonicus*-*Etropus* spp. group was connected to the sardine-sanddab group through the pairings of *S. japonicus* with *S. sagax* and *Citharichthys* spp. The sardine-sanddab group was linked to two other southern groups through intergroup associateships involving *C. xanthostigma*. This species was an associate of *T. mexicanus* in a 3-member southern group and also with *D. laternatus* in a 5-member group. The remaining northern-southern link was formed between a 5-member northern group and a 3-member southern group through the associate relationship of *E. mordax* and *T. mexicanus* (Figure 7).

In 1958 the northern and southern complexes

were linked by associate relationships formed between a 7-member northern group and a 5-member southern group (Figure 7). The relatively high proportion (0.34) of intergroup associates resulted largely from the inclusion of the southern complex species *P. crockeri* in the northern group. It had significant affinities with all taxa except *T. mexicanus* of the southern group. Also, *T. symmetricus* of the southern group formed associate relationships with *E. mordax*, *S. leucopsarus*, and *M. productus* of the northern group. The myctophid *L. ritteri* also had associate links with these 3 species and with *B. ochotensis*. The two groups were further linked by the associate pairing of *E. mordax* and *T. mexicanus* (Figure 7).

In 1959 the northern and southern complexes were connected by the single associate pairing of *E. mordax* and *T. mexicanus*; however, in 1960 a group formed by the northern species *E. mordax* and two southern complex species (*L. ritteri* and *P. crockeri*) was responsible for extensive intercomplex linkage (Figure 7). *E. mordax* formed associate relationships with *Sebastes* spp., *S. leucopsarus*, *L. stilbius*, *M. productus*, *S. sagax*, and *C. fragilis* from 3 northern complex groups and with a 3-member southern group through an associate tie with *T. mexicanus*. The latter species also had a significant affinity with *P. crockeri*. The pairing of *L. ritteri* and *T. symmetricus* further linked the 3-member southern group and the *E. mordax*-*L. ritteri*-*P. crockeri* group. Other intercomplex links were through the associate pairs *L. stilbius*-*P. crockeri* and *L. stilbius*-*T. mexicanus*. Connections between two northern complex groups and two southern coastal complex groups were formed by associate pairings of *C. xanthostigma*-*Symphurus* spp. and *S. sagax*-*E. acuminatus*.

Interannual variability of the constituents and structure of the recurrent groups was more variable than that found in the complexes. In the northern complex, recurrent group analysis of the combined 1954-60 data (Figure 6) produced 4 groups. The largest group contained *B. ochotensis*, *L. stilbius*, *S. leucopsarus*, *M. productus*, and *Sebastes* spp. *Engraulis mordax* formed a group with *C. fragilis* and *C. xanthostigma*; *S. sagax* formed a group with *S. japonicus*; and *T. crenularis* formed a group pair with *I. lockingtoni* (Figure 6). The group diagrams for individual years showed that *E. mordax* and *S. sagax* were closely allied with the 5 members of the LEUROGLOSSUS group and that these 7 taxa were present in each year. In most of the years these taxa formed one or two groups with one or more of the taxa arranged as associates. *T. crenu-*

laris was either included in one of these groups or was absent from the diagram. An exception was in 1959 when it paired with *I. lockingtoni* to form a group, as it did in the combined data set. The sanddabs *C. fragilis* and *C. xanthostigma* were retained as a group for most of the years. Exceptions were in 1956 when they separated to become members of two other flatfish groups and in 1957 when they combined with *S. sagax* and *Citharichthys* spp. to form a 4-member group (Figures 6 and 7).

The 7 principal taxa of the northern complex co-occurred consistently during the seven-year period. The following pairs had significant affinity indices (>0.30) for each of the seven years as well as for the combined data set: *S. sagax*-*E. mordax*, *E. mordax*-*L. stilbius*, *E. mordax*-*Sebastes* spp., *E. mordax*-*M. productus*, *B. ochotensis*-*L. stilbius*, *B. ochotensis*-*S. leucopsarus*, *L. stilbius*-*S. leucopsarus*, *L. stilbius*-*Sebastes* spp., *L. stilbius*-*M. productus*, *S. leucopsarus*-*Sebastes* spp., *Sebastes* spp.-*M. productus*. Two other pairs, *E. mordax*-*S. leucopsarus* and *S. leucopsarus*-*M. productus*, had significant affinity indices in all but one year, when the index fell just short of 0.30.

The high degree of co-occurrence in the 13 pairs listed above was shown by their high affinity indices. For the seven-year series 71% of the indices were above 0.40, 47% were above 0.50, and 8% exceeded 0.60. Affinity indices exceeded 0.40 for each of the seven years in *E. mordax*-*L. stilbius*, *E. mordax*-*M. productus*, *L. stilbius*-*S. leucopsarus*, *L. stilbius*-*Sebastes* spp., *L. stilbius*-*M. productus*, *S. leucopsarus*-*Sebastes* spp., and *Sebastes* spp.-*M. productus*. In *E. mordax*-*Sebastes* spp. the index exceeded 0.50 for all years. The other pair of the northern complex that had significant affinity indices for all seven years was *C. fragilis*-*C. xanthostigma*.

Interannual variability in recurrent group structure was greater in the southern complex than in the northern complex. Recurrent group analysis of the combined seven-year data set produced 5 groups from 18 midwater taxa and *T. symmetricus*. Five other midwater taxa were associates of these groups. Most of these taxa were present in recurrent group analyses of individual years, although group composition and arrangement were highly variable (Figures 6 and 7). In 1954, 1955, and 1959 there were one large group of 5-7 taxa and two smaller groups of 2-3 taxa. In 1957 there were two large groups of 5 and 7 taxa and a 3-member group. The largest group in 1960 contained 4 taxa with connecting links to 4 smaller groups. Group structure in 1956 was the most divergent and was limited

to 5 paired taxa; moreover, only 11 of the 19 southern complex taxa from the 1954-60 combined data set contributed to these groups (Figure 6).

Only the following 6 southern complex pairs had significant indices (> 0.30) for all years: *B. wesethi*-*T. mexicanus*, *Cyclothone* spp.-*V. lucetia*, *Cyclothone* spp.-*C. townsendi*, *V. lucetia*-*D. laternatus*, *V. lucetia*-*T. mexicanus*, and *L. ritleri*-*T. symmetricus*. Of these pairs, only *V. lucetia*-*D. laternatus* had affinity indices higher than 0.40 for all years. Seven other pairs had affinity indices greater than 0.30 for six of the seven years (*B. wesethi*-*V. lucetia*, *B. wesethi*-*S. californiensis*, *Cyclothone* spp.-*T. mexicanus*, *V. lucetia*-*Lampanyctus* spp., *D. laternatus*-*T. mexicanus*, *L. ritleri*-*P. crockeri*, and *L. ritleri*-*S. californiensis*). In all but one of these pairs the nonsignificant affinity index occurred in 1956. Low affinity indices occurred throughout the southern complex in 1956; in a list of 67 taxon pairs, more than half had their lowest index in 1956. Of the mixed northern-southern complex pairs only *E. mordax*-*T. mexicanus* had consistently high affinity indices, ranging from 0.26 to 0.50 for the seven years.

The southern coastal complex was highly variable in the structure and composition of its recurrent groups and associate taxa. In the combined seven-year data set, 4 demersal taxa from 4 different orders formed an isolated group with one associate from a fifth order. Two family taxa, Serranidae and Carangidae (all jacks except *Trachurus* and *Seriola*) formed a second isolated group (Figure 6). Four of the taxa from the large group (*Synodus* spp., *Prionotus* spp., *Ophidion scrippsae*, and *Etrumeus acuminatus*) were persistent annually, occurring as group members or associates in six of the seven years (Figures 6 and 7). The fifth taxon, *Symphurus* spp., was present in only four of the seven years. Another key taxon, Ophidiiformes (all cusk-eels except *O. scrippsae* and *Chilara taylori*, and all brotulas except *Brosomphysis marginata*), was present as a group member or associate in five of the seven years. The Carangidae-Serranidae group was less prominent. These taxa occurred as a group in 1959 and 1960 and in separate recurrent groups in 1956. The thread herrings, *Opisthonema* spp., occurred in recurrent groups in four of the seven years. Gerreidae, the mojarras, appeared in four of the seven years: as a group member with *Opisthonema* spp. in 1954 and 1958 and as an associate in two other years. Pomacentridae (damselfishes other than *Chromis*), *Auxis* spp., and *Syacium ovale* occurred as group members or associates in three of the seven years, and

19 other taxa occurred once or twice during the seven-year period.

Group structure changed markedly from year to year. In 1954, 9 taxa were arranged in 4 groups with one of these (*E. acuminatus*-*Synodus* spp.) connected to the southern complex through an associate linkage between *Synodus* spp. and *Vinciguerria lucetia* (Figure 8). Incidence of southern coastal taxa was anomalously low in 1955, and they did not appear in the recurrent group analysis for that year. The isolated pair, Sciaenidae-*Pleuronichthys verticalis*, had a more northerly coastal distribution. In 1956, 13 taxa formed 5 highly interconnected groups (Figure 6). One of the 3 associate taxa, *O. scrippsae*, was shared by 2 of the groups, and the *Synodus*-*Scorpaena*-*Symphurus* group was linked to the northern complex through a *Symphurus* spp.-*Citharichthys xanthostigma* associateship. In 1957, 5 of the key southern coastal taxa formed a group linked to 5 associates and a 2-member group (Figure 7). The extensive associate linkages of this group to the northern complex were described earlier in this section. In 1958, 8 taxa formed 4 group pairs; 3 of these were interconnected, but there was no associate linkage with the northern or southern complexes. Similarly, in 1959, 12 species formed a cluster of 4 linked groups and an isolated group, with no associate connections to the northern or southern complexes (Figure 7). In 1960, 12 species formed a cluster of 4 interconnected groups and one isolated pair (Figure 7). Two groups within the cluster were connected to the northern complex through associate pairings (*C. xanthostigma*-*Symphurus* spp., *S. sagax*-*E. acuminatus*) with members of two northern complex groups.

The highly variable nature of incidence and co-occurrence of southern coastal taxa was shown in the list of annual affinity indices for selected pairs. Only 3 pairs had significant affinity indices for four of the seven years: *E. acuminatus*-*Synodus* spp., *Prionotus* spp.-Carangidae, and *Prionotus* spp.-*O. scrippsae*. Ranges of indices for the seven-year period were wide, and there was no obvious interannual trend except that values for 1955 were either zero or extremely low for selected pairs.

ENVIRONMENTAL CHANGE AND THE DISTRIBUTION OF RECURRENT GROUPS

The dynamic environmental changes that occurred during 1954-60 in the CalCOFI region markedly affected the distribution of larval fishes. These geographic shifts, in concert with changes in the amount and seasonal extent of spawning, re-

TABLE 4
Percent Change of Incidence of Taxa in the Central Part of the
CalCOFI Survey Area between 1955-56 and 1958-59

	SCal		NBCal		
	In	Off	In	SVB	Off
Northern complex					
LEUROGLOSSUS group					
<i>Bathylagus ochotensis</i>	-8	-16	-2	-2	-4
<i>Leuroglossus stilbius</i>	-16	-24	-33	-20	-21
<i>Stenobranchius leucopsarus</i>	-23	-20	-18	0	-9
<i>Sebastes</i> spp.	-15	-28	-17	-22	-14
<i>Merluccius productus</i>	11	-3	-25	-28	-25
TARLETONBEANIA group					
<i>Tarletonbeania crenularis</i>	-14	-28	-4	0	-3
<i>Ichthyos lockingtoni</i>	-4	-12	-4	-1	-3
CITHARICHTHYS group					
<i>Engraulis mordax</i>	2	12	-4	-9	-4
<i>Citharichthys fragilis</i>	0	0	-4	-3	-1
<i>Citharichthys xanthostigma</i>	0	1	-8	-15	-1
SARDINOPS group					
<i>Sardinops sagax</i>	17	-7	-9	-3	-17
<i>Scomber japonicus</i>	6	1	2	-4	-4
Southern complex					
SYMBOLOPHORUS group					
<i>Bathylagus wesethi</i>	3	19	10	-3	-6
<i>Cyclothone</i> spp.	2	23	6	7	24
<i>Diogenichthys atlanticus</i>	0	0	6	15	17
<i>Lampanyctus ritteri</i>	4	23	-2	-1	-16
<i>Symbolophorus californiensis</i>	3	22	2	0	-2
TRIPHOTURUS group					
<i>Triphoturus mexicanus</i>	15	30	23	23	17
<i>Protomycophum crockeri</i>	0	4	2	-2	-17
<i>Trachurus symmetricus</i>	5	7	-3	-14	-26
CERATOSCOPELUS group					
<i>Ceratospiculus townsendi</i>	1	10	7	4	23
<i>Lampadena urophao</i>	*	2	1	2	8
VINCIGUERRIA group					
<i>Vinciguerria lucetia</i>	9	52	37	29	54
<i>Diogenichthys laternatus</i>	0	0	6	15	17
<i>Goniichthys tenuiculus</i>	*	0	1	3	11
<i>Hygophum atratum</i>	*	*	0	2	5
Southern coastal complex					
SYNODUS group					
<i>Synodus</i> spp.	*	*	0	-5	0
<i>Prionotus</i> spp.	*	*	*	2	*
<i>Ophiodon scrippsae</i>	0	*	1	3	0
<i>Symphurus</i> spp.	2	0	1	-1	0

Abbreviations:

SCal = Southern California (CalCOFI lines 80-97)

NBCal = Northern Baja California (CalCOFI lines 100-117)

In = Inshore (usually <100 km)

Off = Offshore (about 100-400 km)

SVB = Bahía Sebastián Viscaíno

* = No specimens found in region in any year

sulted in changes in the structure and composition of recurrent groups. Distributional shifts for recurrent group taxa are shown in Table 4, which lists the percent change in incidence of larvae between 1955-56 and 1958-59 in five subareas of the CalCOFI survey region. These areas off southern California (SCal) and northern Baja California (NBCal) had the most consistent and equitable monthly sampling effort and greatest environmental effect during the period.

In general, taxa of the northern complex declined, and their southern distributional limits contracted northward during El Niño, while taxa of the southern complex showed a relative increase and a concomitant northward expansion of their northern distributional limits. Members of the LEUROGLOSSUS group, with the exception of *M. productus*, decreased in all five subareas during this period (Table 4). Of the three midwater species, *B. ochotensis* had the smallest decline, with a maximum decrease of 16% in the SCal offshore area. *L. stilbius* decreased in all subareas, and *S. leucopsarus* showed a 43% decrease off SCal. *Sebastes* spp. decreased in all subareas, most notably in the SCal offshore area. *M. productus* decreased consistently in all subareas of NBCal, only slightly in offshore SCal, and showed a substantial increase in the SCal inshore area.

The two taxa of the TARLETONBEANIA group were poorly represented off NBCal and showed only slight decreases there during El Niño (Table 4). They were well represented in the SCal area, particularly offshore, and the decrease there reflected a northward contraction of spawning in these subarctic-transitional species during this period.

Members of the CITHARICHTHYS group decreased in all subareas off NBCal (Table 4). This is particularly noteworthy for the two warm-water sanddab species, whose distributions are concentrated in Bahía Sebastián Viscaíno (SVB) and more southerly shelf areas. *E. mordax* also decreased off NBCal but increased off SCal, particularly in the offshore region, reflecting a northward and seaward expansion of spawning distribution during El Niño.

The two species of the SARDINOPS group have coastal distributions that peak in the SVB area. Both decreased slightly in this area during El Niño (Table 4). *S. sagax* decreased in other areas, particularly in offshore NBCal, but showed a distinct increase in the SCal inshore area. The decrease of *S. sagax* in the four subareas could be attributed to the general decline of the stock during this period,

as well as to El Niño effects. *S. japonicus* also increased slightly in SCal and inshore NBCal.

In the southern complex, the members of the SYMBOLOPHORUS group are midwater taxa that occur principally in offshore areas (Table 3). The two warm-water cosmopolite taxa, *D. atlanticus* and *Cyclothone* spp., increased markedly in the NBCal area, particularly offshore, and the latter taxon showed a strong increase in the SCal offshore region; this indicates a shoreward and northerly expansion of its spawning range (Table 4). The two transitional species *B. wesethi* and *S. californiensis* increased substantially in the SCal offshore area, increased to a lesser degree in the SCal and NBCal inshore areas, and decreased slightly in the NBCal offshore area. *L. ritteri* has a broad subarctic-transitional distribution; it increased in the SCal area, particularly offshore, and decreased off NBCal.

In the TRIPHOTURUS group, the warm-water myctophid *T. mexicanus* occurs relatively infrequently north of Baja California. During El Niño it expanded northward throughout the Southern California Bight, where its incidence increased by 15%-30%; it also increased substantially in the other four areas (Table 4). The two transitional species *P. crockeri* and *T. symmetricus* had less striking changes during El Niño. *T. symmetricus* increased slightly off SCal, but decreased off NBCal, particularly in the offshore region. *P. crockeri* experienced little change off SCal and inshore areas of NBCal, but decreased in the NBCal offshore area. The two members of the CERATOSCOPELUS group are myctophids with offshore distributions, centered off Baja California. During El Niño their incidence increased markedly in the NBCal offshore area, reflecting a shoreward and slight northerly expansion of their spawning distribution (Table 4).

In the VINCIGUERRIA group, *V. lucetia* had the greatest distributional change of all recurrent group taxa during El Niño. It is an abundant eastern tropical Pacific mesopelagic with a usual northern limit of about CalCOFI line 100 (Figure 1) off Ensenada, Baja California. During El Niño it expanded to north of Point Conception, California, showing increases greater than 50% in the offshore areas of SCal and NBCal (Table 4). Although it increased substantially in the inshore areas of NBCal, it increased only slightly in the inshore area of SCal and appeared to be excluded from that area. The other three species are eastern tropical Pacific myctophids with more southerly northern limits; *D. laternus* occurs infrequently north of

Isla Guadalupe, Mexico, and *H. atratum* and *G. tenuiculus* are rarely found north of Punta Eugenia. During El Niño, *D. laternatus* and *G. tenuiculus* increased off NBCal, largely in the offshore area (Table 4). *H. atratum* increased in SVB and in the NBCal offshore area.

Larvae of the SYNODUS group in the southern coastal complex occurred in the shelf regions of SVB and the Punta Abreojos-Cabo San Lázaro Bight to the south. *Symphurus* spp., *O. scrippsae*, and *Synodus* spp. occurred in small numbers on the SCal shelf; only *Symphurus* spp. showed a slight increase in this area during El Niño (Table 4). *Prionotus* spp. and *O. scrippsae* increased slightly in SVB during this period, while *Synodus* spp. and *Symphurus* spp. decreased.

The fine-scale association of selected larval fish taxa and their environment was examined by identifying the temperature-salinity (T-S) characteristics correlated with the presence and absence of these species in a region of mixed water types. The study area for two subarctic-transitional species, *S. leucopsaris* and *T. crenularis*, was bounded by CalCOFI lines 83 to 100, and the area for the two eastern tropical Pacific species, *V. lucetia* and *D. laternatus*, was bounded by lines 100 to 120.

The T-S profiles (Figure 11) represent stations that were either positive or negative for the four species during a period of highly variable oceanographic conditions (1954-60, excluding 1957). These profiles showed a positive correlation between the presence of larvae of the two northern species and cooler, less saline water. Presence of the southern species was correlated with warmer, more saline water in their area. The depth at which the "positive" and "negative" curves were separated was about 150 m, except for *D. laternatus*, where the curves were separated throughout the water column (Figure 11).

The differences in temperature-salinity characteristics associated with the presence or absence of these species reflect the differences in oceanographic conditions before and after the onset of El Niño in 1957. More than two-thirds of all the samples with positive counts for the two subarctic species (*S. leucopsaris* and *T. crenularis*) were taken during 1954-56. Conversely, more than two-thirds of the samples with zero counts for these species were taken in 1958-60.

In the southern area, more than seven-eighths of the samples with positive counts for *V. lucetia* were taken in 1958-60, whereas three-fourths of the samples with zero counts were taken in 1954-56. The data for the other subtropical species, *D. later-*

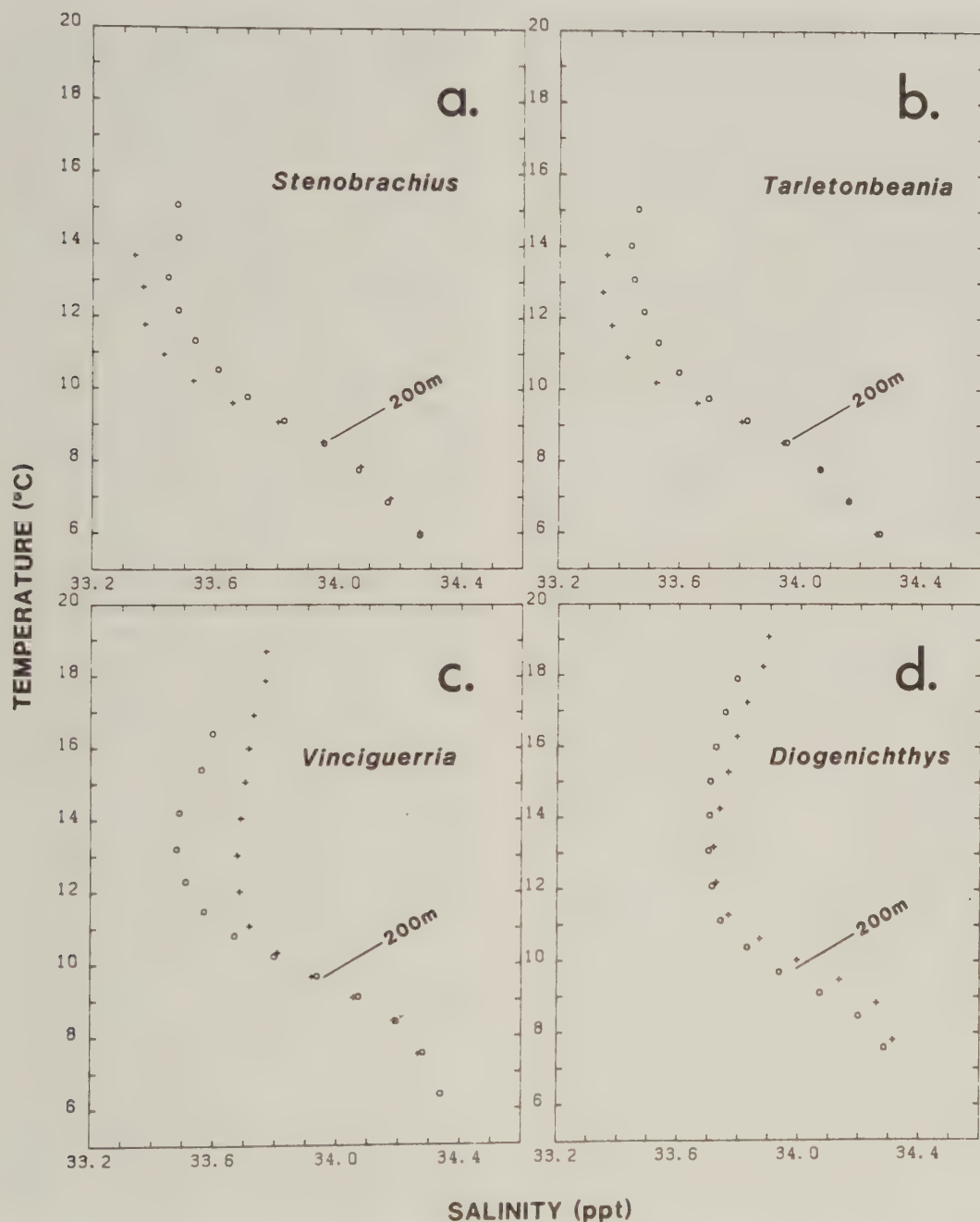


Figure 11. a. Mean temperature-salinity curves depicting differences in watermass characteristics associated with the absence (○) or presence (+) of *Stenobranchius leucopsarus* larvae in CalCOFI net tows. The plots represent combined data from 16 offshore stations on lines 83-100 (see Figure 1) occupied during 1954-60. b. Same as a for *Tarletonbeania crenulans* larvae. The data represented in the figure are from 14 offshore stations on lines 83-100. c. Same as a, for *Vinciguerria luceta* larvae. The data represented in this figure are from 21 offshore stations on lines 100-120. d. Same as a, for *Diogenichthys lateratus* larvae. The data represented in this figure are from 17 offshore stations on lines 103-120.

natus, show less distinction between the pre- and post-1957 periods. Although four-fifths of the samples with positive counts were taken in 1958–60, more than two-thirds of those with zero counts were also taken in that period. Consequently, the T-S curves for both positive and zero counts of *D. laternatus* reflect mainly 1958–60 conditions. The curious separation of these curves below 200 meters is an unexplained feature.

DISCUSSION

The CalCOFI surveys were designed to encompass the areal and temporal limits of the Pacific sardine and its principal ecological associates. The fact that this was accomplished by a monthly sampling program sensitive to mesoscale oceanographic and biological events makes this time series unique. The seven-year period from 1954 to 1960, analyzed in this paper, was of special interest because it contained a major El Niño that was immediately preceded by an anomalously cold period. The recent efforts to reidentify much of the larval fish material from these years and establish a computer data base for it gave us the opportunity to study the structure of fish assemblages in the California Current region during a period of great environmental change.

Recurrent group analysis establishes the co-occurrence of taxa in time and space. When such analysis is applied to an oceanic plankton survey like the CalCOFI sampling program, co-occurrences of larval stages reflect all life-history stages of epipelagic taxa, from egg to adult. Co-occurring taxa experience similar biotic and abiotic environmental conditions and are themselves part of each other's environment. Knowledge of the degree of co-occurrence is a basis for studying trophic relations and competitive interactions between taxa. We view this analysis as a first step in studying the population ecology of these taxa from the standpoint of early life-history stages. Analysis of fluctuations in abundance of these taxa (Smith, Moser, Eber, in prep.) will provide insight into how environment and species interactions affect the populations. Some of these data have been used to estimate population trends of fishery stocks for the past 50 years. These analyses can now be broadened to the ecosystem scale to further define the role of environment, species interaction, and fisheries on the fish stocks of the California Current region.

How well does recurrent group analysis define the larval fish assemblages of the California Current region? Analysis of the pooled data set for

1954–60 identified three major faunal complexes that reflect the transitional nature of the ocean and its zoogeographic components in this region. In the northern complex the CalCOFI surveys define the southern and seaward spawning boundaries of the subarctic-transitional and transitional taxa that make up LEUROGLOSSUS and TARLETON-BEANIA, two groups separated by displaced spawning seasons. The pattern also circumscribes the northern spawning limit for *Merluccius productus* in the LEUROGLOSSUS group⁴. Seaward and latitudinal spawning boundaries for the two major clupeoids (*Engraulis mordax* and *Sardinops sagax*) were also defined by the CalCOFI pattern⁵. Larvae of *E. mordax* were pervasive in the CalCOFI sampling region; this in combination with an extended spawning season ensures that larvae of most common species in the CalCOFI region co-occur with anchovy larvae at some time during the year. Indeed, affinity indices with members of the LEUROGLOSSUS group were consistently high, and *E. mordax* was included as a group member with those species in all but one of the single-year analyses during the seven-year period. This same pervasive areal and temporal distribution pattern appears to have characterized *S. sagax* before the collapse of the stock; however, sardine spawning was centered off central Baja California during 1954–60. In the analysis of the pooled 1954–60 data set, *E. mordax* was grouped with two warm-water sanddab species, and *S. sagax* was paired with *Scomber japonicus*. The sanddab species *Citharichthys fragilis* and *C. xanthostigma* are clearly not "northern" species; however, they were linked to the northern complex through their consistently strong affinities with *E. mordax*, *S. sagax*, and *Sebastes* spp. Likewise, *S. japonicus* is not a "northern" species but was linked to the northern complex through its strong affinity with *S. sagax*.

In contrast to the northern and coastal character of the northern complex, the principal constituents of the southern complex are mesopelagics that inhabit more southerly and offshore waters. Although the taxa were partitioned into 4 groups in the pooled analysis, the various taxa mixed freely and combined to form a variety of groups in analyses of individual years. The 5-member SYMBOLOPHORUS group is faunistically diverse. *Bathylagus wesethi* and *Symbolophorus californiensis* are

⁴Subpopulations of *M. productus* spawn in the Straits of Georgia, British Columbia, and in Puget Sound, Washington.

⁵The degree of genetic interchange between Gulf of California and outer coast stocks of these two species is unknown.

inhabitants of the California Current region, with distributions centered off Point Conception to Punta Eugenia; their latitudinal and inshore-offshore spawning limits are essentially defined by the CalCOFI pattern. The warm-water cosmopolite *Diogenichthys atlanticus* extends into the CalCOFI area between Point Conception and Punta Eugenia, where its latitudinal limits are well defined. *Cyclothone* spp. has a similar distribution in the CalCOFI area; however, it is primarily equatorial, and only its northern spawning limits are defined by the CalCOFI survey pattern. *Ceratoscopelus townsendi* and *Lampadena urophaos* have distributions similar to *D. atlanticus* and *Cyclothone* spp. in the CalCOFI region. They pair to form a separate group because of the extremely close areal overlap and spawning seasonality, with a sharp peak in August.

TRIPHOTURUS is the most zoogeographically disparate group in the southern complex. *Trachurus symmetricus* and *Protomyctophum crockeri* are transitional species with distributions extending to the western Pacific, and are clearly not "southern" species. In the CalCOFI region their larval distributions have broad temporal and spatial overlap with that of the warm-water myctophid *Triphoturus mexicanus*, particularly in the region between Point Conception and Punta Eugenia. *T. mexicanus* also overlaps broadly with *E. mordax*, with whom it forms consistently high intercomplex affinity indices. It may be viewed as a kind of latitudinal mirror image of *E. mordax* in the southern part of the CalCOFI region. The transitional nature of the TRIPHOTURUS group was shown by the strong affinities its members had with taxa of the northern complex and by the inclusion of *T. mexicanus* and *P. crockeri* in northern complex recurrent groups in 1954 and 1958 (Figures 6 and 7).

VINCIGUERRIA is the most faunistically coherent group in the southern complex. The northern spawning boundaries of its 4 eastern tropical Pacific species are clearly defined by the CalCOFI pattern. *V. lucetia* is abundant and widespread off the entire Baja California coast. *D. laternatus* is widespread but less abundant. *Hygophum atratum* and *Gonichthys tenuiculus* are even less abundant, and chiefly south of Punta Eugenia.

The presence of a southern coastal complex in the CalCOFI data set results from the interplay of coastal bathymetry and the survey pattern. Bahía Sebastián Viscaíno and the Punta Abrejos-Cabo San Lázaro Bight are the only large shelf areas in the station pattern. Taxa in this southern coastal complex are the northern representatives of the

shorefish fauna of the tropical-subtropical eastern Pacific. Their northern distributions are sharply curtailed by the narrow shelf of northern Baja California and by the depressed water temperatures of this region that result from coastal upwelling. This complex was isolated from the other complexes in the pooled analysis but formed linkages with the southern and northern complexes in some of the annual analyses.

The descriptions of larval fish assemblages of the CalCOFI region are both informative and conservative. The analysis of pooled data of the northern complex shows the relationship between the subarctic-transitional core group and the pervasive coastal pelagic species with southerly linkages. Likewise the offshore, the California Current region endemic, and the eastern tropical Pacific components of the southern complex are well demonstrated, along with the taxa that bridge the two major complexes. Some of the groupings (e.g., SARDINOPS, CITHARICHTHYS, and TRIPHOTURUS) are not intuitively obvious. Taxa of these groups bind together the divergent fish assemblages of the region by extensive co-occurrence. Annual variation in group composition and in intergroup and associate linkages generally supports the overall scheme described by the pooled data set. Forthcoming analyses of additional yearly surveys and a larger pooled data set will allow further refinement.

The conservative quality of the faunal assemblages is shown by examining the effect of El Niño on recurrent group structure. The cooling trend, which peaked in 1956, resulted in lowered affinity indices among southern-complex species and produced depauperate southern-complex groups. Only about half of the group taxa present in the seven-year pooled analysis were present in 1956. With the onset of the warming trend in 1957 these taxa regained their prominence; northern-complex taxa, however, did not show an analogous decrease in representation as the El Niño peaked in 1958 and 1959, despite lowering of affinity indices for some northern-complex pairs. Neither was there major intermixing of northern and southern recurrent groups resulting from northward and shoreward expansion of spawning of the latter. Taxa of the TRIPHOTURUS group (*T. mexicanus*, *Trachurus symmetricus*, *Protomyctophum crockeri*) were the central figures in intercomplex linkages throughout the seven-year period, because of their inclusion in northern recurrent groups or their extensive associate pairings with northern group members. Intercomplex connections were also

caused by *E. mordax* and *S. sagax*, particularly through affinities of the former with *T. mexicanus*.

The interconnections of northern and southern complexes made through the sanddab *C. xanthostigma* in 1957 and 1960 were an expression of the warm-water distribution of this species and the absence of its indirect connection to the northern complex through *E. mordax*. The same was true for *S. japonicus*, which paired with the flatfish *Etropus* spp. instead of *S. sagax* in 1957. Interestingly, the sanddab recurrent group, *C. xanthostigma* and *C. fragilis*, was isolated from all other groups in the peak El Niño years 1958 and 1959. This was apparently related to the marked reduction of their numbers during this period, the opposite of what one would expect for warm-water species. Perhaps increased larval mortality associated with reduced productivity was the cause.

We anticipated that species assemblages arising from presence-absence techniques like the Fager recurrent group analysis (Fager 1963) would be more robust than those techniques which use the estimates of the quantities of organisms (MacDonald 1975). This is so because within the habitats of these species, spawning products are patchy and the chance co-occurrence of large numbers of two patchy organisms would assume greater importance than may be warranted. Fager (1957) also pointed out that, in analyses based on abundance, inverse quantities of organisms resulting from predation or competition could be misinterpreted by quantitative analysis so as to displace one of the organisms from an assemblage.

One possible disadvantage of the Fager recurrent group analysis relates to the method of resolving ties in the assembly of large groups. It appears that the more ubiquitous of two alternate group members may tend to be eliminated because it could eventually form a larger group than the less ubiquitous alternate. One example was *E. mordax*. Within the LEUROGLOSSUS group *E. mordax* had high affinities with every group member but *Bathylagus ochotensis*. If *E. mordax* had been selected as the member, *B. ochotensis* would have been displaced and made a member of the TARLETONBEANIA recurrent group; *Icichthys lockingtoni* of that group would have been displaced to an associate of that group; CITHARICHTHYS would have been diminished to two group members; and all of the associates of CITHARICHTHYS would have been transferred to LEUROGLOSSUS. Only in 1958 were *E. mordax* and *B. ochotensis* in the same recurrent group.

The northern and southern complexes were pre-

served when recurrent group analysis was applied to the combined 1954–60 data set, using a series of high critical affinity values (0.4, 0.5, 0.6). One can observe in the northern complex diagram (Figure 8) that the removal of the 0.3 links (single lines) leaves only a group of five taxa with an associate and an isolated pair. The southern complex (Figure 10) dissolved similarly into one group of four taxa with several associates. Almost all the diversity is gone when both 0.3 and 0.4 (double) lines are removed, and only two isolated pairs remain when the 0.5 line (triple) is also removed. It appears that in this analysis of larval stages of fish taxa, the critical values of 0.3 maintained the structure of the common fish assemblages and permitted the description of associations like the southern coastal complex, SYNODUS, near the sampling threshold.

Considering the possibilities for chaos with several faunal groups contributing to the California Current region, it appears that the structure of the system is clear when several years are pooled. These seven years were selected because they had two cold years, 1955 and 1956; had two warm years, 1958 and 1959; were bounded by two relatively "normal" years, 1954 and 1960; and were separated by one transitional year, 1957. The recurrent group analysis of 1975 clearly separated the same northern and southern complexes as this set (Loeb et al. 1983). It remains to be seen whether the 1954–60 set can be considered to be representative or whether new forms of assemblages will arise from the other 16 years yet to be analyzed. It is probable that another complex, representative of the central water mass, will be defined from analysis of extended cruises in 1972. Also, it may be possible that more intensive coastal sampling of the recent decade (Barnett et al. 1984; Lavenberg et al. 1986) may define a "northern coastal complex" similar to that found by Gruber et al. (1982) in the Southern California Bight.

Lastly, the distinctions among the complexes are exceedingly clear, considering that the system is embedded in a current which is moving several thousand kilometers each year and mixing with coastal temperate, subarctic, and subtropical waters. There is much to be learned from the study of the necessary physiological, behavioral, and oceanographic mechanisms that maintain these groups of populations in one locale.

ACKNOWLEDGMENTS

This study would not have been possible without the dedicated efforts of many people. We are in-

debted to David Ambrose, Elaine Sandknop, Elizabeth Stevens, and Barbara Sumida for correcting historical data records and reidentifying much of the larval fish material. Richard Charter designed and administered the data base. Cindy Meyer and Larry Zins wrote programs, and Celeste Santos and Debby Snow checked written data and data files. Jim Ryan rewrote the Fager recurrent group analysis in Pascal so that this large data base with several hundred taxa could be analyzed with a microcomputer. For the excellent time series we are indebted to the founders of the CalCOFI program and the many scientists, technicians, and ships' crews who carried it out.

LITERATURE CITED

- Ahlstrom, E.H. 1971. Kinds and abundance of fish larvae in the eastern tropical Pacific, based on collections made on EASTROPAC I. *Fish. Bull. U.S.* 69:3-77.
- . 1972a. Kinds and abundance of fish larvae in the eastern tropical Pacific on the second multivessel EASTROPAC survey, and observations on the annual cycle of larval abundance. *Fish. Bull. U.S.* 70:1153-1242.
- . 1972b. Distributional atlas of fish larvae in the California Current region: six common mesopelagic fishes. *Calif. Coop. Oceanic Fish. Invest. Atlas* 17.
- Allen, L.G. 1985. A habitat analysis of the nearshore marine fishes from southern California. *Bull. South. Calif. Acad. Sci.* 84:133-155.
- Allen, M.J. 1982. Functional structure of soft-bottom fish communities of the southern California shelf. Ph.D. dissertation, Univ. Calif., San Diego.
- Alvarino, A. 1964. Zoogeografía de los Quetognatos, especialmente de la región de California. *Ciencia* 23:51-74.
- Ambrose, D.A., R. Charter, H.G. Moser, and C. Santos. In press, a. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1955. *Southw. Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Tech. Memo.*
- . In press, b. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1960. *Southw. Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Tech. Memo.*
- Anonymous. 1963. CalCOFI atlas of 10-meter temperatures and salinities 1949 through 1959. *Calif. Coop. Oceanic Fish. Invest. Atlas* 1.
- Bakun, A. 1985. Comparative studies and the recruitment problem: searching for generalizations. *Calif. Coop. Oceanic Fish. Invest. Rep.* 26:30-40.
- Bakun, A., and R.H. Parrish. 1982. Turbulence, transport, and pelagic fish in the California and Peru Current systems. *Calif. Coop. Oceanic Fish. Invest. Rep.* 23:99-112.
- Barnett, A.M., A.E. Jahn, P.D. Sertic, and W. Watson. 1984. Distribution of ichthyoplankton off San Onofre, California, and methods for sampling very shallow coastal waters. *Fish. Bull. U.S.* 82:97-111.
- Barnett, M.A. 1983. Species structure and temporal stability of mesopelagic fish assemblages in the central gyres of the North and South Pacific Ocean. *Mar. Biol.* 74:245-256.
- . 1984. Mesopelagic fish zoogeography in the central tropical and subtropical Pacific Ocean: species composition and structure at representative locations in three ecosystems. *Mar. Biol.* 82:199-208.
- Brinton, E. 1962. The distribution of Pacific euphausiids. *Bull. Scripps Inst. Oceanogr.* 8:2:51-270.
- . 1979. Parameters relating to the distributions of planktonic organisms, especially euphausiids in the eastern tropical Pacific. *Prog. Oceanogr.* 8:125-189.
- Chelton, D.B. 1981. Interannual variability of the California Current—physical factors. *Calif. Coop. Oceanic Fish. Invest. Rep.* 22:34-48.
- Chelton, D.B., P.A. Bernal, and J.A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current. *J. Mar. Res.* 40:1095-1125.
- Ebeling, A.W. 1962. Melamphidae I: systematics and zoogeography of the species in the bathypelagic fish genus *Melamphaes* Gunther. *Dana Rep. No.* 58.
- Ebeling, A.W., R.M. Ibara, R.J. Lavenberg, and F.J. Rohlf. 1970. Ecological groups of deep-sea animals off southern California. *Nat. Hist. Mus. Los Ang. Cty. Sci. Bull.* 6.
- Eber, L.E., and N. Wiley. 1982. Revised update and retrieval system for the CalCOFI oceanographic data file. *Southw. Fish. Cent., Natl. Mar. Fish. Serv., NOAA Tech. Memo* 24.
- Ekman, S. 1953. Zoogeography of the sea. Sidgwick and Jackson, London.
- Eschmeyer, W.N., E.S. Herald, and H. Hammann. 1983. A field guide to Pacific coast fishes of North America. Houghton Mifflin Co., Boston.
- Fager, E.W. 1957. Determination and analysis of recurrent groups. *Ecology* 38:586-595.
- . 1963. Communities of organisms. In M.N. Hill (ed.), *The sea*, vol. 2. Interscience, New York, p. 415-437.
- Fager, E.W., and J.A. McGowan. 1963. Zooplankton species groups in the North Pacific. *Science* 140:453-460.
- Fiedler, P.C., R.D. Methot, and R.P. Hewitt. 1986. Effects of California El Niño 1982-1984 on the northern anchovy. *J. Mar. Res.* 44:317-338.
- Gruber, D., E.H. Ahlstrom, and M.M. Mullin. 1982. Distribution of ichthyoplankton in the Southern California Bight. *Calif. Coop. Oceanic Fish. Invest. Rep.* 23:172-179.
- Hickey, B.M. 1979. The California Current System—hypotheses and facts. *Prog. Oceanogr.* 8:191-279.
- Horn, M.H., and L.G. Allen. 1978. A distributional analysis of California coastal marine fishes. *J. Biogeogr.* 5:23-42.
- Hulley, P.A. 1986. A taxonomic review of the genus *Triphoturus* Fraser-Brunner, 1949 (Myctophidae, Osteichthyes) Ann. South Africa Mus. 97(4):71-95.
- Kendall, A.W., Jr., and J. Clark. 1982. Ichthyoplankton off Washington, Oregon, and northern California, April-May 1980. *U.S. Nat. Mar. Fish. Serv., Northwest and Alaska Fisheries Center Processed Report* 82-11, 44 p.
- Kramer, D., M.J. Kalin, E.G. Stevens, J.R. Thrailkill, and J.R. Zweifel. 1972. Collecting and processing data on fish eggs and larvae in the California Current region. *U.S. Dept. Comm. NOAA Tech. Rep. NMFS Circ.* 370:1-38.
- Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer* 173:212-230.
- Lavenberg, R.J., G.E. McGowan, A.E. Jahn, J.H. Petersen, and T.C. Sciarrotta. 1986. Abundance of southern California nearshore ichthyoplankton. *Calif. Coop. Oceanic Fish. Invest. Rep.* 27:53-64.
- Loeb, V.J., 1979. Larval fishes in the zooplankton community of the North Pacific Central Gyre. *Mar. Biol.* 53:173-191.
- . 1980. Patterns of spatial and species abundance within the larval fish assemblage of the North Pacific Central Gyre during late summer. *Mar. Biol.* 60:189-200.
- Loeb, V.J., P.E. Smith, and H.G. Moser. 1983. Recurrent groups of larval fish species in the California Current area. *Calif. Coop. Oceanic Fish. Invest. Rep.* 24:152-164.
- Lynn, R.J. 1986. The subarctic and northern subtropical fronts in the eastern north Pacific Ocean in spring. *J. Phys. Oceanogr.* 16:209-222.
- Lynn, R.J., and J.J. Simpson. In press. California Current system—the seasonal variability of its physical characteristics. *J. Geophys. Res.*
- MacDonald, K.B. 1975. Quantitative community analysis: recurrent group and cluster techniques applied to the fauna of the Upper Devonian Sonyea Group. *New York. J. Geol.* 82:473-499.

- McGowan, J.A., 1971. Ocean biogeography of the Pacific. In B.H. Funnell and W.R. Riedel (eds.), The micropaleontology of oceans. Cambridge University Press, Cambridge, p. 3-74.
- McGowan, J.A., and P.W. Walker, 1979. Structure in the copepod community of the North Pacific central gyre. Ecol. Monogr. 49:195-226.
- Mearns, A.J. 1974. Southern California's inshore demersal fishes: diversity, distribution, and disease as responses to environmental quality. Calif. Coop. Oceanic Fish. Invest. Rep. 17:141-148.
- Miller, D.J., and R.N. Lea. 1972. Guide to the coastal marine fishes of California. Calif. Dept. Fish and Game, Fish. Bull. 157.
- Moser, H.G., and E.H. Ahlstrom. 1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narrow-eyed larvae. Nat. Hist. Mus. Los Ang. Cty. Sci. Bull. 7.
- Mullin, M.M., and E.R. Brooks. 1970. Production of the planktonic copepod *Calanus helgolandicus*. In J.D.H. Strickland (ed.), The ecology of the plankton off La Jolla, California, in the period April through September 1967. Bull. Scripps Inst. Oceanogr. 17, p. 89-103.
- Parin, N.V. 1961. The distributions of deep-sea fishes in the upper bathypelagic layer of the subarctic waters of the northern Pacific Ocean. Tr. Inst. Okeanol. Akad. Nauk SSSR 45:359-378 (In Russian, English abstract).
- Reid, J.L. 1960. Oceanography of the northeastern Pacific Ocean during the last ten years. Calif. Coop. Oceanic Fish. Invest. Rep. 7:77-90.
- Reid, J.L., E. Brinton, A. Fleminger, E.L. Venrick, and J.A. McGowan. 1978. Ocean circulation and marine life. In H. Charnock and G. Deacon (eds.), Advances in oceanography. Plenum, p. 65-130.
- Richardson, S.L., and W.G. Pearcy. 1977. Coastal and oceanic fish larvae in an area of upwelling off Yaquina Bay, Oregon. Fish. Bull. U.S. 75:125-145.
- Richardson, S.L., J.L. Laroche, and M.D. Richardson. 1980. Larval fish assemblages and associations in the north-east Pacific ocean along the Oregon coast, winter-spring 1972-75. Estuarine and Coastal Mar. Sci. 2:671-699.
- Sandknop, E.M., R. Charter, H.G. Moser, and J. Ryan. In press. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1958. Southw. Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Tech. Memo.
- Smith, P.E. 1985. A case history of an anti-El Niño to El Niño transition on plankton and nekton distribution and abundances. In W.S. Wooster and D.L. Fluharty (eds.), El Niño north: Niño effects in the eastern subarctic Pacific Ocean. Washington Sea Grant Program, Univ. of Washington Seattle, p. 121-142.
- Smith, P.E., and R.W. Eppeley. 1982. Primary production and the anchovy population in the Southern California Bight: comparison of time series. Limnol. Oceanogr. 27:1-17.
- Smith, P.E., and R. Lasker. 1978. Position of larval fish in an ecosystem. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 173:77-84.
- Stevens, E.G., R. Charter, H.G. Moser, and M. Busby. In press, a. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1956. Southw. Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Tech. Memo.
- . In press, b. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1959. Southw. Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Tech. Memo.
- Sumida, B.Y., R. Charter, H.G. Moser, and D. Snow. In press, a. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1954. Southw. Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Tech. Memo.
- . In press, b. Ichthyoplankton and station data for California Cooperative Oceanic Fisheries Investigations survey cruises in 1957. Southw. Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Tech. Memo.
- Sverdrup, H.U., M.W. Johnson, and R.H. Fleming. 1942. The oceans: their physics, chemistry, and general biology. Prentice-Hall, Englewood Cliffs, N.J.
- Tsuchiya, M. 1982. On the Pacific upper-water circulation. J. Mar. Res. 40(Suppl):777-799.
- Venrick, E.L. 1979. The lateral extent and characteristics of the North Pacific central environment at 35°N. Deep-Sea Res. 26:1153-1178.
- Willis, J.M. 1984. Mesopelagic fish faunal regions of the northeast Pacific. Biol. Oceanogr. 3:167-185.
- Wisner, R.L. 1976. The taxonomy and distribution of lanternfishes (family Myctophidae) in the eastern Pacific ocean. Navy Oceanographic Research Development Activity, Washington, D.C.
- Wyllie, J.G. 1966. Geostrophic flow of the California Current at the surface and at 200 meters. Calif. Coop. Oceanic Fish. Invest. Atlas 4.

APPENDIX

Larval Fish Taxa That Constitute Recurrent Groups, Associates, and Affiliates, from Pooled CalCOFI Survey Data, 1954-60

Taxon	Incidence (11,551 total)	Associate group	Taxon	Incidence	Associate group
Northern Complex			CITHARICHTHYS		
LEUROGLOSSUS			recurrent group		
recurrent group			<i>Engraulis mordax</i>	5,097	
<i>Leuroglossus stilbicus</i>	3,010		<i>Citharichthys fragilis</i>	821	
<i>Bathylagus ochotensis</i>	1,172		<i>Citharichthys xanthostigma</i>	980	
<i>Stenobranchius leucopsarus</i>	2,439		Associates (members or associates of other recurrent groups)		
<i>Sebastes</i> spp.	4,485		<i>Leuroglossus stilbicus</i>	3,010	LEUROGLOSSUS
<i>Merluccius productus</i>	3,027		<i>Stenobranchius leucopsarus</i>	2,439	LEUROGLOSSUS
Associates (members or associates of other recurrent groups)			<i>Sebastes</i> spp.	4,485	LEUROGLOSSUS
<i>Engraulis mordax</i>	5,097	CITHARICHTHYS	<i>Merluccius productus</i>	3,027	LEUROGLOSSUS
<i>Citharichthys stigmaeus</i>	1,322	CITHARICHTHYS	<i>Citharichthys stigmaeus</i>	1,322	LEUROGLOSSUS
<i>Sardinops sagax</i>	1,477	SARDINOPS	<i>Sardinops sagax</i>	1,477	SARDINOPS
<i>Tarletonbeania crenularis</i>	1,044	TARLETONBEANIA	<i>Triphoturus mexicanus</i>	4,648	TRIPHOTURUS
Affiliates			Associates (unique)		
Osmeridae	4		<i>Citharichthys</i> spp.	904	
<i>Nansenia</i> spp.	3		Affiliates		
<i>Bathylagus milleri</i>	7		<i>Argentina sialis</i>	438	
<i>Bathylagus pacificus</i>	54		Gobiesocidae	4	
<i>Valenciennellus stellatus</i>	1		Atherinidae	18	
Macrouidae	40		<i>Syngnathus</i> spp.	29	
<i>Brosomphycis marginata</i>	80		<i>Ophiodon elongatus</i>	7	
Hexagrammidae	4		<i>Zaniolepis</i> spp.	39	
<i>Oxylebius pictus</i>	38		<i>Caulolatilus princeps</i>	55	
Cottidae	250		Sciaenidae	499	
<i>Scorpaenichthys</i>			Clinidae	118	
<i>marmoratus</i>	53		Gobiidae	592	
Agonidae	78		<i>Sarda chiliensis</i>	18	
Cyclopteridae	41		<i>Peprilus simillimus</i>	216	
<i>Lyopsetta exilis</i>	485		Blennioidei	5	
<i>Microstomus pacificus</i>	147		Pleuronectiformes	109	
<i>Parophrys vetulus</i>	297		<i>Citharichthys sordidus</i>	424	
<i>Pleuronichthys coenosus</i>	51		<i>Paralichthys californicus</i>	244	
<i>Pleuronichthys decurrens</i>	22		<i>Hippoglossina stomata</i>	258	
<i>Psettichthys melanostictus</i>	22		<i>Pleuronichthys</i> spp.	100	
TARLETONBEANIA			<i>Pleuronichthys ritteri</i>	19	
recurrent group			<i>Pleuronichthys verticalis</i>	178	
<i>Tarletonbeania crenularis</i>	1,044		<i>Hypsopsetta guttulata</i>	5	
<i>Icichthys lockingtoni</i>	633		SARDINOPS recurrent group		
Associates (members or associates of other recurrent groups)			<i>Sardinops sagax</i>	1,477	
<i>Bathylagus ochotensis</i>	1,172	LEUROGLOSSUS	<i>Scomber japonicus</i>	513	
<i>Stenobranchius leucopsarus</i>	2,439	LEUROGLOSSUS	Associates (members or associates of other recurrent groups)		
<i>Sebastes</i> spp.	4,485	LEUROGLOSSUS	<i>Sebastes</i> spp.	4,485	LEUROGLOSSUS
Affiliates			<i>Merluccius productus</i>	3,027	LEUROGLOSSUS
<i>Leuroglossus schmidtii</i>	3		<i>Engraulis mordax</i>	5,097	CITHARICHTHYS
<i>Danaphos oculatus</i>	1		Affiliates		
<i>Chauliodus macouni</i>	421		<i>Girella nigricans</i>	17	
<i>Diaphus</i> spp.	628		<i>Hypsopops rubicundus</i>	2	
Bathymasteridae	1		<i>Sphyræna argentea</i>	107	
Pholididae	1		<i>Semicossyphus pulchrum</i>	5	
<i>Icosteus aenigmaticus</i>	6		(continued)		
<i>Glyptocephalus zachirus</i>	62				

APPENDIX (continued)

Larval Fish Taxa That Constitute Recurrent Groups, Associates, and Affiliates, from Pooled CalCOFI Survey Data, 1954-60

Taxon	Incidence	Associate group	Taxon	Incidence	Associate group
Southern Complex			Associates (unique)		
SYMBOLOPHORUS			<i>Lampanyctus</i> spp.	966	
recurrent group			<i>Stomias atriventer</i>	803	
<i>Bathylagus wesethi</i>	1,935		Affiliates		
<i>Cyclothone</i> spp.	1,784		Anguilliformes	163	
<i>Diogenichthys atlanticus</i>	734		Stomiiformes	50	
<i>Lampanyctus ritteri</i>	2,288		<i>Nansenia crassa</i>	326	
<i>Symbolophorus californiensis</i>	966		<i>Bathylagus</i> spp.	29	
Associates (members or associates of other recurrent groups)			<i>Bathylagus nigrigenys</i>	9	
<i>Protomyctophum crockeri</i>	2,303	TRIPHOTURUS	Gonostomatidae	3	
<i>Triphoturus mexicanus</i>	4,648	TRIPHOTURUS	<i>Diplophos taenia</i>	93	
<i>Melamphaes</i> spp.	1,309	TRIPHOTURUS	<i>Ichthyococcus</i> spp.	165	
<i>Trachurus symmetricus</i>	2,095	TRIPHOTURUS	Sternoptychidae	428	
<i>Vinciguerria lucetia</i>	4,288	VINCIGUERRIA	<i>Bathophilus</i> spp.	34	
<i>Diogenichthys laternatus</i>	2,204	VINCIGUERRIA	Myctophiformes	2	
<i>Ceratoscopelus townsendi</i>	988	CERATOSCOPELUS	Evermannellidae	10	
Associates (unique)			<i>Diogenichthys</i> spp.	250	
<i>Paralepididae</i>	772		<i>Hygophum</i> spp.	248	
Affiliates			<i>Loweina rara</i>	82	
<i>Microstoma microstoma</i>	176		<i>Myctophum aurolaterna-</i>	30	
<i>Tactostoma macropus</i>	31		<i>tum</i>		
<i>Aristostomias scintillans</i>	45		Antennariidae	1	
<i>Idiacanthus antrostomus</i>	161		Moridae	5	
Alepocephalidae	1		<i>Physiculus</i> spp.	20	
Scopelarchidae	327		<i>Bregmaceros</i> spp.	60	
<i>Scopelosaurus</i> spp.	36		Carapidae	11	
<i>Myctophum nitidulum</i>	268		<i>Macroramphosus gracilis</i>	6	
<i>Centrobranchus</i> spp.	1		Fistularidae	1	
<i>Electrona rissoi</i>	4		Scorpaenidae	6	
<i>Poromitra</i> spp.	111		<i>Seriola</i> spp.	3	
Trachipteridae	145		Uranoscopidae	5	
<i>Sebastolobus</i> spp.	45		Gempylidae	20	
Apogonidae	11		<i>Thunnus albacares</i>	10	
Chiasmodontidae	294		Nomeidae	20	
<i>Isopsetta isolepsis</i>	1		<i>Citharichthys platophrys</i>	1	
VINCIGUERRIA			<i>Bothus</i> spp.	24	
recurrent group			Balistidae	1	
<i>Vinciguerria lucetia</i>	4,288		TRIPHOTURUS		
<i>Diogenichthys laternatus</i>	2,204		recurrent group		
<i>Gonichthys tenuiculus</i>	537		<i>Protomyctophum crockeri</i>	2,303	
<i>Hygophum atratum</i>	444		<i>Triphoturus mexicanus</i>	4,648	
Associates (members or associates of other recurrent groups)			<i>Trachurus symmetricus</i>	2,095	
<i>Bathylagus wesethi</i>	1,935	SYMBOLOPHORUS	Associates (members or associates of other recurrent groups)		
<i>Cyclothone</i> spp.	1,784	SYMBOLOPHORUS	<i>Bathylagus wesethi</i>	1,935	SYMBOLOPHORUS
<i>Lampanyctus ritteri</i>	2,288	SYMBOLOPHORUS	<i>Cyclothone</i> spp.	1,784	SYMBOLOPHORUS
<i>Symbolophorus californiensis</i>	966	SYMBOLOPHORUS	<i>Lampanyctus ritteri</i>	2,288	SYMBOLOPHORUS
<i>Melamphaes</i> spp.	1,309	SYMBOLOPHORUS	<i>Symbolophorus californiensis</i>	966	SYMBOLOPHORUS
<i>Vinciguerria lucetia</i>	4,288	VINCIGUERRIA	<i>Melamphaes</i> spp.	1,309	SYMBOLOPHORUS
<i>Diogenichthys laternatus</i>	2,204	VINCIGUERRIA	<i>Vinciguerria lucetia</i>	4,288	VINCIGUERRIA
Myctophidae	1,078	VINCIGUERRIA	<i>Diogenichthys laternatus</i>	2,204	VINCIGUERRIA
<i>Ceratoscopelus townsendi</i>	988	CERATOSCOPELUS	<i>Myctophidae</i>	1,078	VINCIGUERRIA
<i>Engraulis mordax</i>	5,097	CITHARICHTHYS	<i>Ceratoscopelus townsendi</i>	988	CERATOSCOPELUS
			<i>Engraulis mordax</i>	5,097	CITHARICHTHYS

(continued)

APPENDIX (continued)

Larval Fish Taxa That Constitute Recurrent Groups, Associates, and Affiliates, from Pooled CalCOFI Survey Data, 1954-60

Taxon	Incidence	Associate group	Taxon	Incidence	Associate group
Affiliates			Affiliates		
<i>Nansenia candida</i>	104		<i>Ophidion scrippsae</i>	195	
<i>Aulopus</i> spp.	1		<i>Symphurus</i> spp.	353	
<i>Lampanyctus regalis</i>	164		Associates (unique)		
Exocoetidae	18		<i>Etrumeus ocreatus</i>	172	
<i>Cololabis saira</i>	177		Affiliates		
<i>Medialuna californiensis</i>	47		<i>Albula vulpes</i>	1	
<i>Oxyjulis californica</i>	23		<i>Opisthonema</i> spp.	13	
Scombridae	57		Engraulidae	5	
<i>Tetraodon lineatus</i>	417		<i>Anotopterus pharao</i>	1	
CERATOSCOPELUS			<i>Porichthys</i> spp.	1	
recurrent group			Lophiidae	1	
<i>Ceratospilus townsendi</i>	988		Ophidiiformes	318	
<i>Lampadena urophysa</i>	307		<i>Chilara taylori</i>	62	
Associates (members or associates of other recurrent groups)			Hemiramphidae	2	
<i>Bathylagus wesethi</i>	1,935	SYMBOLOPHORUS	<i>Scorpaena</i> spp.	111	
<i>Cyclothone</i> spp.	1,784	SYMBOLOPHORUS	Serranidae	190	
<i>Vinciguerra lucetia</i>	4,288	VINCIGUERRIA	Priacanthidae	1	
<i>Triphoturus mexicanus</i>	4,648	TRIPHOTURUS	Carangidae	81	
Affiliates			<i>Seriola lalandi</i>	118	
<i>Notoscopelus resplendens</i>	227		<i>Coryphaena hippurus</i>	77	
<i>Hygophum reinhardtii</i>	111		Gerreidae	34	
<i>Hygophum proximum</i>	2		Haemulidae	48	
<i>Notolychnus valdiviae</i>	21		Mullidae	6	
Ceratioidei	105		Pomacentridae	75	
<i>Scopeloberyx robustus</i>	3		<i>Chromis punctipinnis</i>	125	
<i>Scopelogadus mizolepis</i>	165		<i>Mugil</i> spp.	16	
<i>Howella brodiei</i>	1		Labridae	549	
<i>Brama</i> spp.	39		<i>Halichoeres</i> spp.	24	
Southern Coastal Complex			<i>Hypsoblennius</i> spp.	235	
SYNODUS			Trichiuridae	266	
recurrent group			<i>Euthynnus</i> spp.	3	
<i>Synodus</i> spp.	402		<i>Scomberomorus</i> spp.	7	
<i>Prionotus</i> spp.	132		<i>Auxis</i> spp.	56	
			<i>Etropus</i> spp.	70	
			<i>Syacium ovale</i>	22	
			<i>Xystreurys tirolepis</i>	32	
			Tetraodontidae	1	

**NMFS, Southwest Fisheries Center, Honolulu Laboratory, Honolulu, Hawaii:
Insular Resources Investigation**

Bruce C. Mundy

News about the early life history research at the NMFS Honolulu Laboratory was included in the first 1986 issue of the section's newsletter (vol. 7, no. 1). Since that report, new projects have begun and progress has been made on the continuing studies described previously.

Among the new projects not described earlier, George Boehlert and William Watson (Marine Ecological Consultants, Encinitas, California) are studying the distribution of ichthyoplankton at Johnston Atoll (lat. 16°, long. 169°), a very isolated small island southwest of the Hawaiian chain. Johnston Atoll is interesting because larvae of island associated fish species collected there must be autochthonous, an assumption that cannot be corroborated at most other islands, which are parts of chains or archipelagos. The ichthyoplankton collections at the atoll, collected in November 1984, are valuable for studies of retention and recruitment of larvae in island environments. Boehlert presented part of these data in a paper at the recruitment session of the December AGU/ASLO Ocean Sciences meeting in San Francisco.

David Somerton is investigating the biology of the nehu, *Encrasicholina purpureus*, a small anchovy important as bait in the Hawaiian tuna fishery. Somerton and Kevin Landgraf have obtained estimates of nehu population size in Pearl Harbor using the egg production method developed at the egg production method developed at the NMFS Southwest Fisheries Center laboratory in La Jolla. From weekly sampling of nehu eggs, larvae and adults in the harbor, yielding information about fecundity, spawning frequency, sex ratios and egg abundance, they estimate that the spawning stock averaged 1.55 tons, ranging between 0.58 and 3.91 tons, between May 1 and October 9, 1986.

They have also found that nehu may alternate periods of frequent spawning lasting several weeks with periods of infrequent spawning. Potential relationships between spawning frequency and food (zooplankton) abundance are being investigated; nehu fecundity seems to be correlated with Ocrustacean zooplankton abundance on a weekly time scale. Ultimately, this study is intended to determine if freshwater input into the harbor influences nehu stock size, and how planned alterations of that input will affect the nehu population. In conjunction with that survey, Russell Ito, at our Kewalo Basin laboratory, is developing techniques for spawning nehu and rearing their larvae. Somerton and Ito hope to find morphological indicators of age in nehu larvae that can be used in studies of growth and mortality in the Pearl Harbor populations. The reared nehu larvae will also be used in physiological studies planned for the future.

A cruise of the *Townsend Cromwell* is planned during May 1987 to compare the efficiency of light traps, neuston trawls and larger midwater trawls of small mesh as means of capturing juvenile reef fishes. We will use light traps developed in Australia by Peter Doherty. This study follows preliminary work conducted by Donald Kobayashi, a graduate student at the University of Hawaii who participated in the April 1986 cruise of the vertical distribution study. Don set small light traps in the vicinity of standard NMFS Honolulu Laboratory night-light fishing gear, and was very successful in collecting a variety of juvenile nearshore fishes. These juveniles have not been successfully collected with the 1 m² or smaller plankton nets used on our cruises. While light traps have been used frequently in freshwater environments, their use in open ocean areas is relatively new. We hope that this will be a productive technique for sampling larger larvae and juveniles, and for obtaining live specimens of juvenile reef fishes for experimental purposes.

In addition to the work on nehu, the Kewalo Basin laboratory has also been the site of research on live

larvae of other species. Tom Kazama and James Uchiyama are preparing a manuscript on the validation of using daily otolith growth rings for aging of larvae skipjack tuna, *Katsuwonis pelamis*. The validation was determined by using otoliths from reared larvae of known ages. Kazama has continued the work on skipjack and mahimahi, *Coryphaena hippurus*, reported in the earlier newsletter. Recent research has centered on the effects of temperature on the growth and survival of mahimahi larvae. He has also been rearing larvae of the taape, *Lutjanus kasmira*, to obtain information about growth and culture techniques that could be applied to deeper living snapper species which are commercially important in Hawaii. The aging of taape larvae using daily otolith rings has been validated.

The research reported in the earlier newsletter included two long-term projects at our laboratory: surveys of the fisheries resources at seamounts to the north of the Hawaiian Islands, and a study of the vertical distribution of fish larvae at Oahu. Sampling at Hancock Seamount (lat. 30°, long. 179°) has continued, with bongo samples collected in July to obtain larval *Beryx splendens* for age analysis using otoliths, and with neuston samples collected in October to obtain more larval armorhead, *Pseudopentaceros wheeleri*.

Bruce Mundy presented a poster entitled "Larval development of the alfonsin, *Beryx splendens* (Berycidae, Beryciformes)" at the 66th annual meeting of the American Society of Ichthyologists and Herpetologists in Victoria, B.C. The alfonsin larvae were identified from newly hatched reared specimens of known parentage, and from the meristics of large specimens. Identifying characters for *Beryx* larvae include the precocious development of elongate pelvic rays and dorsal spines, sparse pigment in an unusual pattern, and an S-shaped intestine about half the standard length. Head spine development is diagnostic for larger larvae. Within the Beryciformes, *Beryx* larvae are most similar to larvae Melamphroids. Larval beryciforms show a rich diversity of

developmental characters that may provide much information on their interrelationships once the polarity of the character states can be established.

Boehlert and Mundy are continuing the study of the vertical distribution of ichthyoplankton around Oahu reported in the earlier newsletter. All four of the planned seasonal cruises (September 1985, December 1985, April 1986 and June 1986) have been completed. Analysis of the samples from the first cruise has given some interesting preliminary results. Tuna larvae are abundant in surface waters nearshore, as reported by previous workers in the region. Larvae of some nearshore fish families are most abundant nearshore, including the Lutjanidae and the highly abundant Gobiidae. Others, such as the Labridae, are more abundant in deeper water away from the immediate vicinity of the island than in areas near shore. While larvae of most mesopelagic species were most abundant 20-100 m deep in offshore areas, certain species, such as the myctophid *Lampadena urophaos*, were very abundant in the upper 20 m near the island. These few shallowly occurring mesopelagic species seem to account for the high abundances of oceanic larvae found near the island by previous researchers. Sorting and identification of the fish larvae from the remaining cruises is continuing.

FOUR NEW MYSIDS FROM CALIFORNIAN COASTAL WATERS

Masaaki Murano and James R. Chess

ABSTRACT

One new genus and four new species of Mysidacea collected from Californian coastal waters are described. *Amathimysis trigibba*, new species, is unique in having three tubercles on the carapace and is further distinguished from other species of the genus by the antennal scale, mandibular palp, fifth male pleopod, and uropod. This is the first record of the genus occurring on the Pacific coast. *Acanthomysis californica*, new species, is recognized as a new species by the smooth abdominal somites and the shape and armature of the telson. *Acanthomysis brunnea*, new species, is distinguished by the shape of the rostral plate, the slender antennal scale, the slender side lobe of the fourth male pleopod, and the shape and armature of the telson. The new genus *Hippacanthomysis* is distinguished from allied genera of the tribe Mysini by having an expanded and knife-shaped first segment of the exopod of the fourth male pleopod.

The species described herein are based on specimens collected during ecological investigations in Californian coastal waters by the National Marine Fisheries Service of the United States. In this paper we describe 4 new species, one of which is placed in a new genus. The type specimens are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

Amathimysis trigibba, new species

Figs. 1, 2

Material.—21 February 1974: 4 adult ♂♂, 3.0 mm, 4 adult ♀♀, 2.8–3.2 mm, 3 immature ♂♂, 3 immature ♀♀; Fishermans Cove, Catalina Island, California (33°27'N, 118°30'W); depth 10 m; collected with small hand dredge fitted with plankton netting pushed along the bottom by a diver.—April 1974: 3 adult ♂♂, 3.5 mm, 2 immature ♂♂; Isthmus Reef, Catalina Island, California; depth 15 m; collected with mesh bag.—24 February 1981: 3 adult ♀♀, 2.9 mm, 2 immature ♂♂, 2.8, 3.1 mm; Isthmus Reef, Catalina Island, California; depth 15 m; collected with mesh bag.—26 September 1983: 3 adult ♂♂, 2.7–3.0 mm, 2 immature ♂♂, 2.6, 2.8 mm, 4 immature ♀♀, 2.4–2.6 mm; Fishermans Cove, Catalina Island, California; depth 12 m; collected with hand dredge.

Type Series.—Holotype (USNM 228061), adult ♀ with embryos, 2.9 mm; allotype (USNM 228062), adult ♂, 3.0 mm; and paratypes (USNM 228063), 2 adult ♀♀, both 2.9 mm (one of which was dissected) and 2 immature ♂♂, 2.8, 3.1 mm. Holotype and paratypes were collected on 24 February 1981, at Isthmus Reef, Catalina Island, California, and allotype on 26 September 1983, at Fishermans Cove, Catalina Island, California.

Description.—General form rather robust, conspicuous constriction present between thorax and abdomen.

Frontal margin of carapace produced anteriorly in broadly rounded rostral plate, extending to base of antennular peduncle; lateral margins of rostrum evenly convex, partially covering eyestalks in female, eyestalks exposed in male (Fig. 1B, C); posterior margin of carapace emarginate, exposing last thoracic somite; 3 small tubercles on dorsal surface located between frontal margin of carapace and cervical sulcus (Fig. 1A–C).

Eyes developed, slightly longer than broad; cornea wider than stalk (Fig. 1B, C).

Antennular peduncle short, more robust in male than female; in female, segment 1 about as long as broad, segment 2 short, segment 3 longer than broad (Fig. 1B); in male, segment 3 broader than segment 2 and longer than preceding 2 segments combined, with single simple seta on inner distal margin, downward produced processus masculinus hirsute (Fig. 1C).

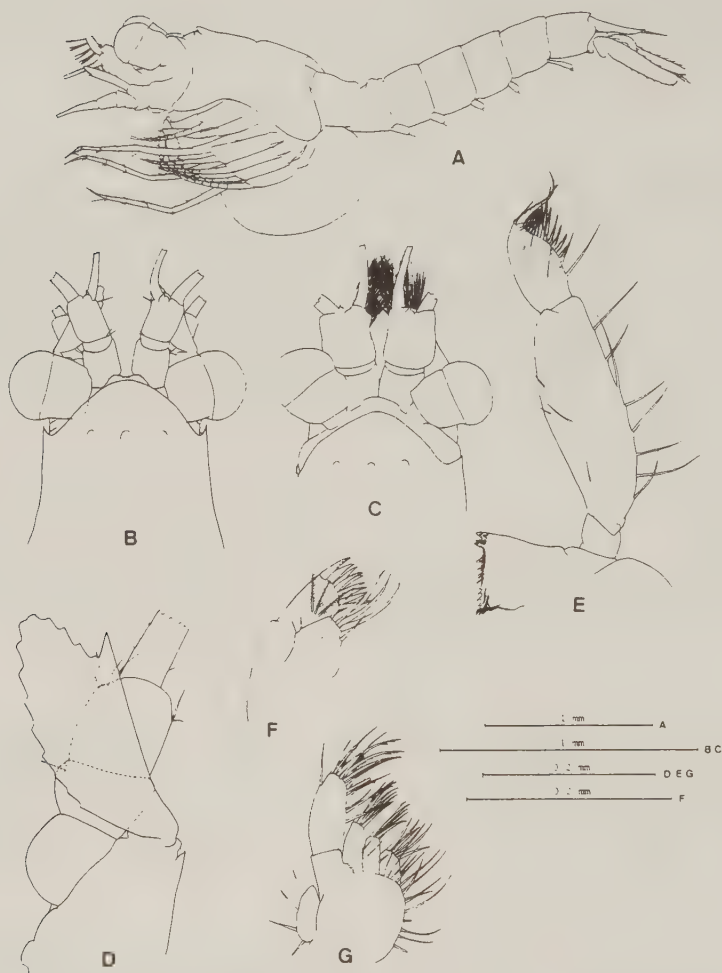


Fig. 1. *Amathimysis trigibba*, new species. A, adult female (2.9 mm) in lateral view; B, anterior end of adult female; C, anterior end of adult male; D, antenna (♀); E, mandible (♀); F, maxillule (♀); G, maxilla (♀).

Antenna with scale short, lanceolate, one-fifth of its length extending beyond distal margin of antennular peduncle (Fig. 1B), less than 3 times as long as broad, apex extending far beyond lateral triangular denticle, outer margin proximal to denticle naked, slightly concave near base, convex inner margin and outer margin distal to denticle setose; terminal lobe slightly wider than long, no distal suture; antennal peduncle shorter than antennular peduncle, extending to distal three-fourths of scale, segment 2 shortest; sympod without pointed outer distal corner (Fig. 1D).

Labrum with broadly rounded frontal margin.

Mandible simple, similar to that of *Amathimysis gibba* Brattegard; palp 3-segmented, segment 2 slender, 3 times as long as broad, armed sparsely with



Fig. 2. *Amathimysis trigibba*, new species. A, endopod of first thoracic limb (♀); B, second thoracic limb (♀); C, fifth thoracic limb (♀); D, first pleopod (♂); E, fourth pleopod (♂); F, fifth pleopod (♂); G, distal part of modified seta on fifth segment of endopod of fifth pleopod (♂); H, telson and uropod (♀).

slender setae, segment 3 two-fifths as long as segment 2, twice as long as broad, armed with about 13 barbed spines arranged in regular row (Fig. 1E).

Maxillule with about 9 strong spines on distal margin of outer lobe, inner lobe with 3 long stout setae and 2 shorter setae on distal margin, 2 short setae on outer margin and 2 short setae (one is broken in Fig. 1F) on inner margin (Fig. 1F).

Maxilla with exopod small, with only 5 setae along outer margin; endopod rather slender, 2-segmented, segment 2 twice as long as broad (Fig. 1G).

First thoracic endopod with small endite armed with 4 setae at apex, merus as long as carpo-propodus and dactylus combined, armed with 5 strong barbed setae on inner margin, claw longer than dactylus, serrated on distal third of concave margin (Fig. 2A).

Second thoracic limb with exopod 8-segmented, outer distal margin of basal

plate rounded, without denticles; endopod slender, sparsely setose, merus 5 times as long as broad, almost equal to combined length of carpo-propodus and dactylus, dactylus more than twice as long as broad, terminating in straight claw a little longer than dactylus (Fig. 2B).

Fifth thoracic limb with exopod 8-segmented, with rounded outer distal margin of basal plate; endopod slender, merus slightly curved inwardly, 1.8 times as long as ischium, carpus about half length of merus, segmented by oblique articulation from 2-segmented propodus (Fig. 2C).

Sixth abdominal somite as long as preceding one (Fig. 1A), posterior margin somewhat produced posteriorly and covering basal part of telson in dorsal view (Fig. 2H); all abdominal somites without developed pleural plate (Fig. 1A).

Marsupium composed of 2 pairs of oostegites, posterior pair considerably larger than anterior one.

Pleopods of male bilobed, natatory; first pair with endopod reduced to unsegmented lobe, exopod 6-segmented (Fig. 2D); second to fourth pairs with 6-segmented exopod and endopod being of equal length, each segment of each limb with simple plumose seta on either side of distal margin (Fig. 2E); fifth pair modified, endopod 7-segmented and much longer than exopod, segments 6 and 7 armed with pair of slightly modified setae, distally naked and thicker than ordinary setae, outer setae of segments 3, 4, and 5 furnished with coarse spinules on distal one-third with short terminal portion naked (seta from segment 4 broken but showing apparently similar modification); exopod extending beyond segment 4 of endopod, 6-segmented, without modified setae (Fig. 2F, G). Pleopods of female reduced to simple lobe, fifth pair elongated, twice as long as preceding pair (Fig. 1A).

Uropod rather short; endopod longer than exopod, less than twice as long as telson, without spines near statocyst (Fig. 2H).

Telson 1.1 times longer than last abdominal somite, 1.4 times as long as broad; lateral margins naked, proximal two-thirds convex and distal one-third concave, distal one-fifth subparallel; distal margin transverse, one-fifth of maximum width at base, armed with 2 pairs of spines, inner pair two-fifths of telson length and 6–7 times as long as outer pair (Fig. 2H).

Remarks.—Morphological features of the carapace, mouth parts, thoracic appendages, and telson leave no doubt that the new species belongs to the genus *Amathimysis*. Until now, the genus consisted of 6 species, *A. gibba* Brattegard, 1969, *A. polita* Brattegard, 1974, *A. cherados* Brattegard, 1974, *A. brattegardi* Stuck and Heard, 1981, *A. brasiliiana* Băcescu, 1984 (= *Katerythrops (Amathimysis) brasiliiana*) and *A. serrata* Murano, 1986. All these species have been recorded from coastal waters of the Gulf of Mexico and the Caribbean Sea (e.g., Băcescu and Ortiz, 1984; Brattegard, 1969, 1974a, b; Modlin, 1984; Stuck and Heard, 1981; Murano, 1986). That this new species was collected from the Pacific coast of California is of great interest in the zoogeography of mysids.

This species is easily distinguished from the other 6 species by the 3 tubercles on the carapace. Characteristics such as the antennal scale with a long apical lobe, the mandibular palp with the second segment armed sparsely with slender setae, the fifth male pleopod coarsely plumate on outer distal end of segments 3–5, and the endopod of the uropod longer than the exopod are available as distinguishable points from the other species.

Băcescu (1984) and Băcescu and Ortiz (1984) treated *Amathimysis* as a subgenus within the genus *Katerythrops*, though they did not give any comments. In the shape of the telson and the modified fifth male pleopod, *Amathimysis* is allied

to *Katerythrops*, but the modification of the fifth male pleopod of *Amathimysis* is of a different form than that of *Katerythrops* (Murano, unpublished); moreover, the former genus differs morphologically from the latter in the constriction between the thorax and abdomen, the tubercles on the carapace, and the shape of the mouthparts. These characters should be sufficient to allow *Amathimysis* to stand as a valid genus.

Etymology.—The species is named after the 3 humps on the carapace.

Ecological Note.—This species was collected from several locations along the northwest shore of Catalina Island, California, at depths from 5–23 m. It was most abundant within the suspended detritus layer just over sand/silt substrata but it also occurred among low benthic algae growing on rocks. At night it ventured at least several meters into the water column where it occurred in densities about 8.5 per m³; here it was preyed upon by most of the nocturnal species of fishes occurring in that habitat (Hobson and Chess, 1976).

Acanthomysis californica, new species

Figs. 3, 4

Material.—25 March 1982: 1 adult ♂, 11.3 mm (holotype, USNM 228056), 1 adult ♀, 13.7 mm (allotype, USNM 228057); 36°55.9'N, 122°27.0'W; collected with a Tucker trawl from 119 m where the bottom depth was 143 m.

Description.—Carapace short anteriorly, exposing entire eyestalks, with frontal margin produced into triangular rostral plate; apex more narrowly rounded in male; anterolateral corners rounded; posterior margin emarginate, exposing last thoracic somite (Fig. 3A–C).

Eyes large, extending to distal margin of antennular peduncle segment 2; cornea semiglobular, wider than stalk; stalk without papilliform process on dorsal surface (Fig. 3B, C).

Antennular peduncle more robust in male than female, in male, segment 1 slightly longer than segment 3, while in female, segment 1 clearly longer (Fig. 3B, C).

Antennal scale setose all round, lanceolate, 6 times as long as broad, extending to distal margin of antennular peduncle in male and beyond it in female; distal suture present (Fig. 3D); antennal peduncle three-fourths as long as scale, segment 2 longest, nearly twice as long as segment 3; sympod with spinous process on outer distal corner (Fig. 3D).

Labrum with long, acute frontal process (Fig. 3E).

Maxillule with humplike process armed with several small spines on middle of outer margin of outer lobe (Fig. 3G).

Mandible, maxilla, and first and second thoracic endopods showing no remarkable characteristics (Fig. 3F, H–J).

Endopods of third to eighth thoracic limbs with carpo-propodus 4-segmented (Fig. 4A); exopod of thoracic limbs 8-segmented in first and eighth pairs and 9-segmented in second to seventh pairs.

Female with 2 pairs of oostegites.

Abdominal somites smooth, without folds, furrows, or spine rows (Fig. 3A).

Pleopods of female rudimentary, increasing in length posteriorly; fifth pair very slender, with small proximal lobe, more than twice as long as first pair. Pleopods of male similar to those of female except fourth pair; fourth pair biramous, endopod short, unsegmented, less than half length of exopod, exopod (tip of setae) extending to middle of last abdominal somite, 2-segmented, proximal segment 6

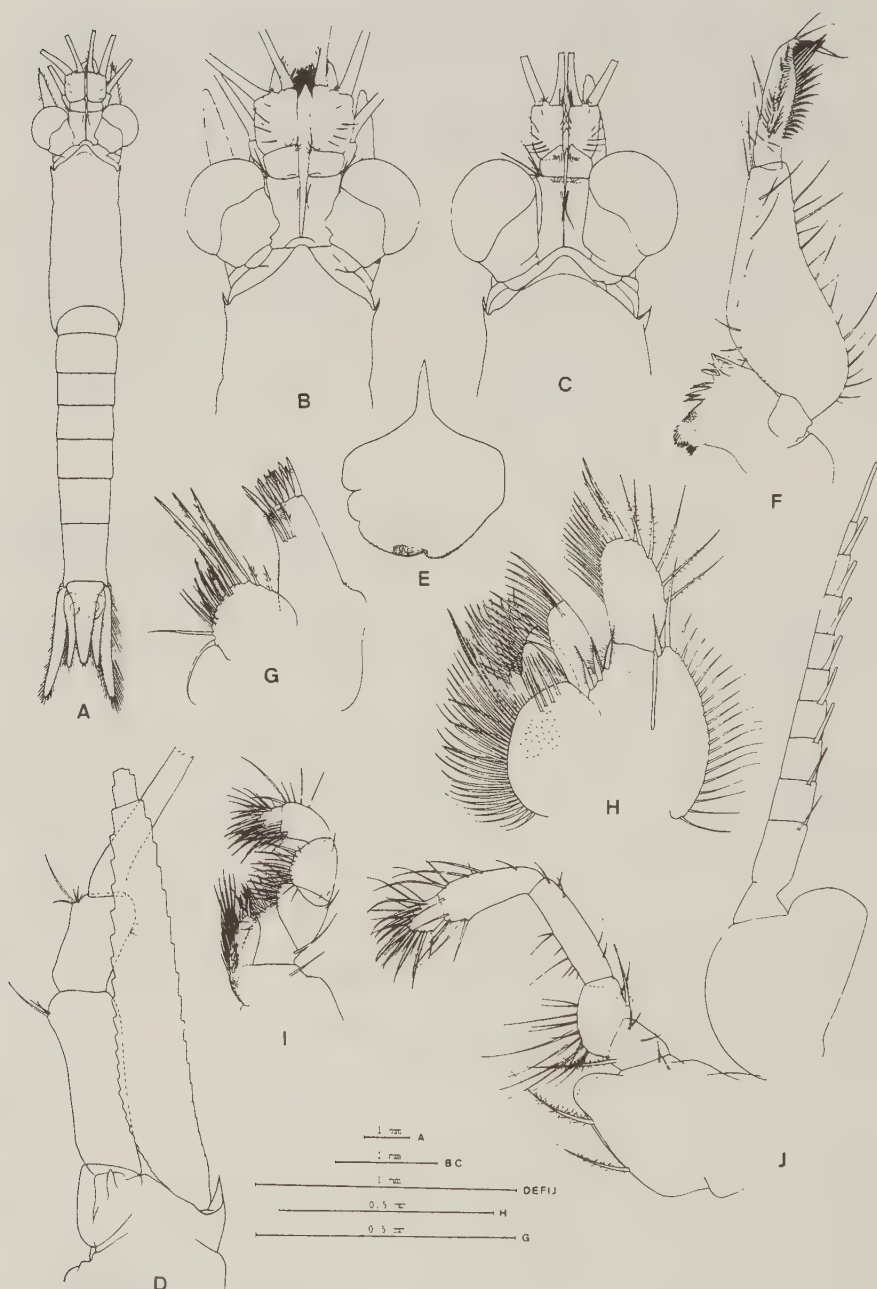


Fig. 3. *Acanthomysis californica*, new species. A, adult male (11.3 mm) in dorsal view; B, anterior end of adult male; C, anterior end of adult female; D, antenna (♂); E, labrum (♀); F, mandible (♂); G, maxillule (♂); H, maxilla (♂); I, endopod of first thoracic limb (♂); J, second thoracic limb (♂).



Fig. 4. *Acanthomysis californica*, new species. A, one of anterior thoracic endopods (♂); B, penis; C, fourth pleopod (♂); D, uropod (♂); E, telson (♂).

times as long as distal segment, inner distal margin with long simple plumose seta being 2.5 times as long as distal segment, seta of outer margin minute, distal segment more than twice as long as broad, with 2 unequal terminal setae furnished with fine spinules on distal half, longer seta nearly half length of exopod, with indistinct suture near its base, shorter seta four-fifths as long as longer one.

Uropod slender; exopod outwardly curved, more than 8 times as long as broad, 1.5 times longer than endopod; endopod tapering, extending slightly beyond apex of telson, with 4 or 5 spines on inner margin of statocyst region (Fig. 4D).

Telson 1.2 times as long as last abdominal somite, twice as long as broad, narrowing abruptly near base, distal four-fifths elongate and triangular; distal margin truncate, narrow, with 2 pairs of spines, outer pair more than twice as long as inner; lateral proximal margin armed with 5 rather large spines, these separated by unarmed region from distal series of spines in which 14 or 15 larger spines are separated by groups of 1–4 smaller spines, these smaller spines gradually increasing in length distally (Fig. 4E).

Remarks.—The genus *Acanthomysis* has been mainly recognized by the characteristics of the antennal scale and fourth male pleopod (Ii, 1964); the antennal scale has a rounded tip and is furnished with setae along the entire margin; and the fourth male pleopod bears a 2-segmented exopod furnished with 2 terminal setae.

Recently, Holmquist (1979, 1980, 1981a, b) reviewed the genus and concluded that this genus was heterogeneous. According to her, the true *Acanthomysis* (*Acanthomysis sensu stricto*), for which *A. longicornis* (Milne Edwards, 1837) is the type

species, consists of only 6 species, and the other species must be referred to genera other than *Acanthomysis*. For their reception, she established 6 genera: *Pacificacanthomysis*, *Alienacanthomysis*, *Exacanthomysis*, *Disacanthomysis*, *Xenacanthomysis*, and *Holmesimysis*, and reestablished one genus, *Orientomysis*. Nevertheless, as many as 28 species remain as "incertae sedis."

The present new species resembles the genus *Acanthomysis* sensu stricto in the following characters: (1) the abdominal somites bear no folds, furrows, or spine rows; (2) the endopod of the third to eighth thoracic limbs has the carpo-propodus divided into 4 subjoints; (3) the endopod of the uropod has 4 or 5 spines on the inner margin near the statocyst; and (4) the telson abruptly narrows near the base, where the lateral margin is armed with 5 spines, this being separated by an unarmed part from the distal series of spines.

However, this species is not in agreement with the diagnosis of *Acanthomysis* sensu stricto given by Holmquist (1981b) in the following respects: (1) the body is not hispid; (2) the proximal lobe of the pleopods is small; (3) the fourth male pleopod bears a long seta on the inner distal end of the proximal segment of the exopod; and (4) the telson has a truncate distal end.

Holmquist (e.g., 1981b) regarded oostegites of the female as an important character in mysid taxonomy. In the present study, however, these structures could not be examined in detail because only a single specimen was available.

In the present incomplete state of revision of the genus *Acanthomysis* sensu lato, we think it better that this species be referred to the genus *Acanthomysis* sensu lato.

Etymology.—The species is named after the locality in which it was collected.

Acanthomysis brunnea, new species

Figs. 5, 6

Material.—21 September 1978; 3 adult ♀♀, 17.4 mm (2 specimens damaged); Albion Cove, Mendocino County, California (39°14'N, 123°47'W); depth 12 m; collected with hand net.—8 December 1978; 3 adult ♂♂, 18.9 mm (2 specimens damaged); from the stomach of a blue rockfish, *Sebastes mystinus*; Albion Cove, California.—11 May 1982; 2 adult ♂♂ (16.1, 13.3 mm), 2 adult ♀♀ with embryos in marsupium (15.7, 15.3 mm); Albion Cove, California; depth 10 m; collected with hand net.

Type Series.—Holotype (USNM 228058), adult ♂, 16.1 mm; allotype (USNM 228059), adult ♀, 15.3 mm; paratypes (USNM 228060), 1 adult ♂, 13.3 mm and 1 adult ♀, 15.7 mm. All collected on 11 May 1982, at Albion Cove, California.

Description.—Carapace with frontal margin produced anteriorly into triangular rostral plate with pointed apex, covering proximal portion of eyestalks and antennular peduncles, lateral margins of rostrum nearly straight, converging about a right angle (Fig. 5A, B); anterolateral corners bluntly pointed; posterior margin emarginate, exposing last thoracic somite dorsally (Fig. 5C).

Eyes well developed, reniform, extending beyond distal margin of segment 2 of antennular peduncle, without papilliform process on stalk; cornea hemispherical, wider than stalk (Fig. 5A, B).

Antennular peduncle more robust in male than female, segment 3 of male longer than preceding 2 segments combined, with processus masculinus well developed, equal in length to segment (Fig. 5A), segment 3 of female armed with 6 long setae on distal margin below inner flagellum and with 5 short setae at anteromedial corner (Fig. 5B).

Antennal scale long, extending beyond antennular peduncle by half its length in female and by two-fifths in male, more than 7 times as long as broad, setose on entire margin, distal segment longer than wide; antennal peduncle half length



Fig. 5. *Acanthomysis brunnea*, new species. A, anterior end of adult male; B, anterior end of adult female; C, adult male (16.1 mm) in lateral view; D, antenna (♂); E, mandible (♂); F, maxillule (♂); G, maxilla (♂); H, endopod of first thoracic limb (♂); I, endopod of second thoracic limb (♂).

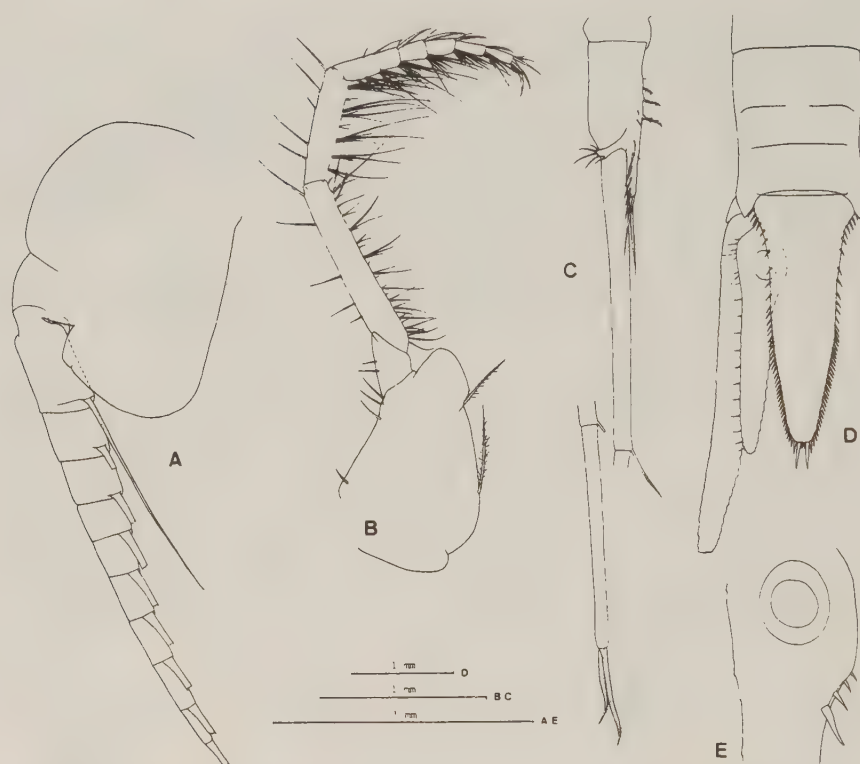


Fig. 6. *Acanthomysis brunnea*, new species. A, exopod of second thoracic limb (♂); B, endopod of third thoracic limb (♂); C, fourth pleopod (♂); D, posterior end of adult male; E, proximal part of endopod of uropod (♂).

of scale, 3-segmented, segment 2 longest; sympod with strong denticle at outer distal corner (Fig. 5D)

Labrum with long, acute frontal projection.

Other mouthparts and first and second thoracic endopods showing no remarkable characteristics (Fig. 5E-I).

Endopods of third to eighth thoracic limbs with carpo-propodus 5-segmented, each of distal 4 subjoints armed with serrated seta on outer distal margin, subjoint 1 longer than subjoints 2 and 3 combined, with 4 groups of long setae on inner margin (Fig. 6B); exopod of thoracic limbs 8-jointed in first pair, 9-jointed in second to eighth pairs, no denticles on rounded outer distal margin of basal plate (Fig. 6A).

Marsupium composed of 2 pairs of ordinary oostegites and 1 rudimentary pair.

Last thoracic somite and abdominal somites 2-6 with 2 transverse folds, abdominal somite 1 with 3 folds (Fig. 5C).

Pleopods of female rudimentary, unsegmented, increasing in length from first pair to fifth pair, fifth pair twice as long as first. Male pleopods similar to those of female except fourth pair; fourth pair biramous, endopod unjointed, short and narrow, terminating in seta, side lobe well developed, slender, 3 times as long as broad, exopod very long, extending to middle of telson, segment 1 more than 4

times as long as endopod, 1.5 times as long as segment 2, armed with seta on inner distal margin, segment 2 terminating in 2 unequal strong setae with rows of spinules (Fig. 6C).

Uropod slender, endopod a little longer than telson, tapering, armed on inner margin near statocyst with 4 spines increasing in length distally; exopod nearly 1.5 times as long as endopod, curved outwards, with distal margin truncate (Fig. 6D, E).

Telson 1.7 times longer than last abdominal somite, 2.5 times as long as broad, triangular with narrow distal margin, distal margin one-eighth of maximum width at base, with 2 pairs of spines, outer being longest among marginal spines of telson and inner being shortest, lateral margin with concave proximal half and straight distal half, with about 35 subequal spines more widely spaced on proximal half (Fig. 6D).

Remarks.—The new species has the following characters: (1) each abdominal somite has 2 or 3 transverse folds; (2) the labrum has a long, acute frontal process; (3) the exopod of the fourth pereopod of the male is very long, reaching the middle of the telson, and the endopod bears a slender, laterally extending side-lobe; (4) the telson is furnished with subequal spines along the whole length of the lateral margin; and (5) the marsupium is composed of 2 pairs of ordinary postegites and one rudimentary pair. The combination of these characters is incompatible with any species of *Acronictomys* sensu stricto or of the six genera which were separated from *Acronictomys* sensu lato and established by Holmquist (1979, 1980, 1981a, b).

As already noted in "Remarks" of the previous species, many species still remain in *Acronictomys* sensu lato. The present species is also distinguishable from these species by the characters mentioned above.

In the present state it is considered that this species should also be assigned to *Acronictomys* sensu lato.

Etymology.—One of the authors (Chen), who was the collector, originally designated this species as "Big Brown." The specific name is derived from it.

Ecological Note.—When alive this species has rich brown pigmentation that closely matches the brown algal (*Laminaria* and *Verucryx*) that dominate the habitat where it is found. Typically it is seen in well-formed schools of 30–50 and adults that actively swim within 1–30 cm of algal-covered boulders. This strong-swimming species occurs at depths of 6–15 m along the open coast where heavy seas prevail. Adults have been seen in this habitat during all seasons. From microscopic analysis of the stomach contents of ten individuals we found that 76.7% (a estimated volume) was composed of crustacean fragments. Most of the identifiable fragments were from gammaridean amphipods but fragments of calanoid and harpacticoid copepods were also present. Diatoms and algal fragments comprised about 4% of their diet and the remaining portion was composed of undetermined material.

Hippasteriopsis, new genus

Diagnosis.—Thoracic and abdominal somites smooth, without long furrows or spine rows. Eyes well developed reniform. Antennal scale lanceolate, entire margin serrate, with distal spine. Labrum with long, acute frontal process. Endopods of thoracic limbs 3–8 with uropereopods 4-segmented. All pereopods of female and male except fourth pair of male rudimentary, unsegmented, with small side-lobe. Endopod of fourth male pereopod 3-segmented, segment 1 long, gradually becoming wider as a distance three-fourths of its length, segment 2 cylindrical,

terminating in 2 strong, barbed setae. Telson narrowing abruptly for proximal one-third, then linguiform for distal two-thirds; lateral margin armed with about 10 rather large spines on proximal part and with grouped spines on linguiform part, each spine group composed of larger spine followed by 1–8 smaller ones; distal end broadly rounded, furnished with 2 pairs of spines, outer pair twice as long as inner. Uropod rather short, inner margin of statocyst region of endopod with about 13 spines increasing in length distally.

Remarks.—Within related genera, such as *Acanthomysis*, *Neomysis*, etc., there are no described species that possess the unique knife-shaped fourth pleopod of the male. Besides this characteristic, the new genus should also be distinguished from related genera by the shape and armature of the telson, a cluster of fine setae on the apex of the penis, and the endopod of the uropod shorter than the telson.

Etymology.—One of the authors (Chess) originally designated this species as “Sea Horse Mysid.” The generic name is derived from it.

Hippacanthomysis platypoda, new genus, new species

Figs. 7, 8

Material.—26 September 1978; 2 immature ♀♀ (badly damaged); Cone Rock, Albion, Mendocino Cove, California (39°14.4'N, 123°46.9'W); collected with an air lift.—26 September 1978; 2 adult ♀♀ (badly damaged); Cone Rock, Albion, California.—7 July 1983; 1 adult ♂, 10.6 mm, 1 adult ♀, 12.2 mm; Albion, California; collected from over coarse sand at a depth of 19 m with hand net.

Type Series.—Holotype (USNM 228064), adult ♂, 10.6 mm; allotype (USNM 228065), adult ♀, 12.2 mm. Both collected on 7 July 1983, at Albion, California.

Description.—Carapace produced anteriorly in triangular rostral plate, in male, apex narrowly rounded and lateral margin of rostrum slightly concave, in female, apex rather broadly rounded and lateral margins straight or slightly convex (Fig. 7A, B); posterior margin emarginate, exposing last thoracic somite (Fig. 7C).

Eyes developed, with cornea hemispherical, slightly wider than stalk, papilliform process absent on stalk (Fig. 7A, B).

Antennular peduncle more robust in male than female, male segment 3 equal to segment 1 in length, as long as broad, with large processus masculinus (Fig. 7A); female segment 3 with seta at middle of inner margin, 2 long setae at inner distal corner, and 5 short setae at base of inner flagellum (Fig. 7B).

Antenna with scale longer than antennular peduncle, entire margin setose, 4.5 times as long as broad, distal suture present; distal two-thirds of inner margin nearly straight and proximal one-third convex, distal two-thirds of outer margin convex and proximal one-third slightly concave; antennal peduncle somewhat longer than half length of scale, 3-segmented, segment 2 longest, nearly twice as long as broad; sympod with strong tooth on anterodistal corner (Fig. 7D).

Labrum with long, acute frontal projection (Fig. 7E).

Mandibular palp with segment 3 two-thirds as long as segment 2 and furnished with about 25 setae arranged regularly along outer margin (Fig. 7F).

Maxillule with swelling over proximal half of outer margin of outer lobe (Fig. 7G).

Maxilla and first and second thoracic endopods similar to those of *Acanthomysis* (Figs. 7H, 8B, C).

Endopods of thoracic legs 3–8 with 4-subdivided carpo-propodus (Fig. 8D). Thoracic exopod 9-segmented in second to seventh pairs and 8-jointed in first and eighth pairs.

Female with 2 pairs of oostegites.

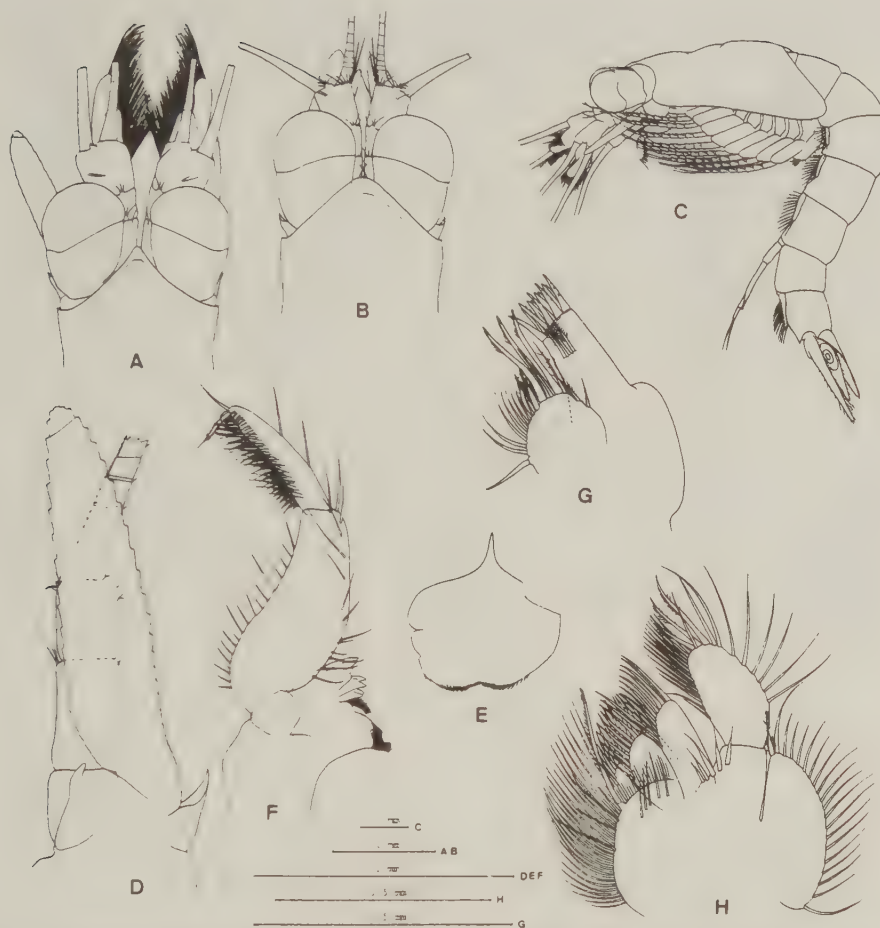


Fig. 7. *Hippacanthomysis platypoda*, new genus, new species. A, anterior end of adult male; B, anterior end of adult female; C, adult male (10.6 mm) in lateral view; D, antenna (♂); E, labrum (♂); F, mandible (♂); G, maxillule (♂); H, maxilla (♂).

Penis elongate, elliptical, with about 11 short spines sparsely arranged on posterior margin and 2 long barbed setae on anterior margin near apex; apex with cluster of fine setae and 6 naked long setae (Fig. 8A).

Abdominal somites smooth, without furrows, folds, or spines (Fig. 7C).

Pleopods of female rudimentary, fifth pair twice as long as first. First to third and fifth pleopods of male reduced to short, single lobe as in female; fourth pleopod of male biramous, extending beyond distal end of abdominal somite 6, exopod well developed, 2-segmented, segment 1 long and flattened, knife-shaped, 3 times longer than endopod, less than 5 times as long as maximum breadth, inner margin smooth, proximal half straight and distal half slightly convex, outer margin strongly convex in distal half, minutely crenulate, distal end armed with pair of short setae, segment 2 cylindrical, 5 times as long as broad, one-fourth as long as segment 1, terminating in 2 subequal, strong, barbed setae 2.5 times as long as segment, endopod short and unsegmented, with small proximal lobe (Fig. 8E).



Fig. 8 *Hippacanthomysis platypoda*, new genus, new species. A, penis; B, first thoracic limb (♂); C, second thoracic limb (♂); D, eighth thoracic limb (♂); E, fourth pleopod (♂); F, uropod (♀); G, telson (♂).

Uropod rather short, entire margin setose; endopod shorter than telson, tapering, armed on inner margin near statocyst with 13 spines increasing in length distally; exopod 1.3 times longer than endopod (Fig. 8F).

Telson large, 1.7 times longer than abdominal somite 6, 1.5 times longer than maximum width, narrowing abruptly near base forming slight constriction at one-third its length from base, distal two-thirds linguiform; proximal one-third of lateral margin sparsely armed with 8–10 spines, distal two-thirds armed with 10 or more longer spines with 1–8 smaller spines between them; apex with 2 pairs of spines with outer pair being twice as long as inner (Fig. 8G).

Remarks.—As noted above, the new species is easily distinguished from allied species by the curious form of the fourth male pleopod.

Etymology.—The name of the species refers to the shape of the fourth male pleopod.

Ecological Note.—This species has been found at depths of 6–20 m and only in close proximity to coarse sandy substrata. It usually occurs in groups of 10–30 individuals that appear relatively inactive, often hovering only a few cm from the bottom. While hovering, their bodies are usually bent into an upright sinuous curve with the head highest, in a manner reminiscent of a swimming sea horse. In the field, the males can often be distinguished by their dark brown pigmentation and the females by their light greenish hue. This species occurs along the outer coast exposed to strong surge.

LITERATURE CITED

- Băcescu, M. 1984. *Katerythrops* s. gen. *Amathimysis brasiliiana* n. sp. and *Mysidopsis sankarankuttyi* n. sp. of the NE Brazilian littoral waters.—*Revue Roumaine de Biologie, série Biologie Animale* 29: 3–7.
- , and M. Ortiz. 1984. Contribution to the knowledge of the Mysidacea (Crustacea) of the Cuban insular shelf waters.—*Travaux du Muséum d'Histoire Naturelle Grigore Antipa* 26: 15–23.
- Brattegard, T. 1969. Marine biological investigations in the Bahamas. 10. Mysidacea from shallow water in the Bahamas and southern Florida. Part 1.—*Sarsia* 39: 17–106.
- . 1974a. Additional Mysidacea from shallow water on the Caribbean coast of Colombia.—*Sarsia* 57: 47–86.
- . 1974b. Mysidacea from shallow water on the Caribbean coast of Panama.—*Sarsia* 57: 87–108.
- Hobson, E. S., and J. R. Chess. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California.—*Fishery Bulletin, United States* 74: 567–598.
- Holmquist, C. 1979. *Mysis costata* Holmes, 1900, and its relations (Crustacea, Mysidacea).—*Zoologische Jahrbücher, Abteilung für Systematik, Ökologie, und Geographie der Tiere* 106: 471–499.
- . 1980. *Xenacanthomysis*—a new genus for the species known as *Acanthomysis pseudomacropsis* (W. M. Tattersall, 1933) (Crustacea, Mysidacea).—*Zoologische Jahrbücher, Abteilung für Systematik, Ökologie, und Geographie der Tiere* 107: 501–510.
- . 1981a. *Exacanthomysis* gen. nov., another detachment from the genus *Acanthomysis* Czerniavsky (Crustacea, Mysidacea).—*Zoologische Jahrbücher, Abteilung für Systematik, Ökologie, und Geographie der Tiere* 108: 247–263.
- . 1981b. The genus *Acanthomysis* Czerniavsky, 1882 (Crustacea, Mysidacea).—*Zoologische Jahrbücher, Abteilung für Systematik, Ökologie, und Geographie der Tiere* 108: 386–415.
- Ii, N. 1964. Fauna Japonica, Mysidae (Crustacea).—*Biogeographical Society of Japan, Tokyo*. Pp. i–x, 1–610.
- Modlin, R. F. 1984. Mysidacea from the Florida Middle Ground, northeast Gulf of Mexico, with descriptions of three new species of *Heteromysis* and a key to the Heteromysini of the western Atlantic.—*Journal of Crustacean Biology* 4: 278–297.
- Murano, M. 1986. Three new species of Mysidacea from Saint Croix, Virgin Islands.—*Crustaceana* 50: 133–145.
- Stuck, K. C., and R. W. Heard. 1981. *Amathimysis brattegardii*, a new peracarid (Crustacea: Mysi-

dacea) from continental shelf waters off Tampa Bay, Florida.—*Journal of Crustacean Biology* 1: 272–278.

RECEIVED: 9 December 1985.

ACCEPTED: 10 June 1986.

Addresses: (MM) Tokyo University of Fisheries, 4-5-7 Konan, Minato-ku, Tokyo 108, Japan; (JRC) Southwest Fisheries Center, Tiburon Laboratory, National Marine Fisheries Service, 3150 Paradise Drive, Tiburon, California 94920.

Ocean climate influences on groundfish recruitment in the California Current

Jerrold Norton
NMFS, Southwest Fisheries Center
Monterey, California

1. Introduction

In this study, patterns of rockfish (genus Sebastes) recruitment variation are shown to be similar to patterns of variation in physical parameter values which describe the rockfishes' environment. The patterns of similarity occur at interannual and longer scales in the 1965 - 1980 period. Although it is important to obtain detailed knowledge of the rockfishes' complete reproductive cycle, including physiological and behavioral adaptations of the young-of-the-year, the approach used here does not depend on having this knowledge.

Studies that link groundfish recruitment success to variation in the physical environment are not new (Ketchen 1956, Templeman 1972, Cushing 1973, Parrish et al. 1981). A number of interesting relationships have been at least partially illuminated. It is hoped that the present investigation will augment the ongoing exploration process that will lead to scientifically based resource management methods.

The focus of the present study is on the large amplitude recruitment fluctuations that remain apparent years and even decades later in the data obtained from commercial fishery samples. The course of the investigation was determined by the following considerations and assumptions.

1. Because of specific adaptations, rockfish population size and structure reflect physical environmental events occurring during the life history

of the population's members (Darwin and Wallace 1858). It is unlikely that co-occurring species can react identically to the range of physical variability occurring in the California Current environment.

2. Probable recruitment success of discrete cohorts of a given species of rockfish can be inferred from catch-age (catch-at-age) composition data derived from otolith (sagittae) readings for a population subset (Hightower and Lenarz 1986, Henry 1986). Imprecision in determining the calendar year of otolith initiation (fishes first year) increases as specimen age increases (Boehlert and Yoklavich 1984).

3. Time series of physical environmental measurements exist that delineate events of diel to decadal time scales. These may have amplitudes of several standard deviation units and may extend over tens of degrees of latitude. (Moore and Robinson 1984, Norton et al. 1985, Chelton et al. 1982). This study is focused on events of interannual and longer time scales because these events are easiest to define and rockfish recruitment variability at these scales is evident in catch-age composition data.

4. Because of uncertainties in aging and the lack of knowledge concerning the effects of environmental change on all stages of rockfish development, the best chance of showing relationships will be found by examining physical conditions during the first year of the fishes' life (Hjort 1914, Hunter 1982). Extremes in first year success (as determined from catch-age composition data) and physical events are important as possible single factor maxima that stand above "noise" that obscures underlying relationships. The rockfish parturition date is taken as January first. So, the calendar year is taken as the fishes' first year.

5. The effects of variation in any particular physical parameter on the young-of-the-year is unknown. So, the approach used in this study is to describe each year in terms of several physical parameters. Because of the reduction of quantitative time series into three bins ("+", "0" and "-"), short time series and qualitative nature of some of the data sets, pattern matching is emphasized.

The major data relationships are seen in Table 1 which organizes the information into binned data series to emphasize common patterns. The physical data are binned by numerical magnitude into three groups relative to the long term means. In general, the bins are labeled "+" for above average or positive anomaly, "0" for a defined average range where random anomaly might be assumed and "-" for below average or negative anomaly. Extremes are labeled "++" and "=-." Widow (*S. entomelas*) and chilipepper (*S. goodei*) rockfish recruitment and zooplankton abundance data series

are given in Table 1 with the highest values indicated by "W," "C" and "Z" respectively. Asterisks show extremes and lowercase letters indicate above average values. The "x" symbol indicates low values of recruitment or abundance. For all series "n" means that the data for this period is not available. Relationships between high first year survival (population recruitment) and various physical parameters are shown for widow and chilipepper rockfish (RF) in Table 1. Row 12 of Table 1 gives a summation of the physical parameters and may be taken as a combined physical indicator. Note that widow RF and chilipepper RF have most successful recruitment under different environmental conditions. Widow RF recruitment appears enhanced during "warm" years which have positive values in row 12 and chilipepper RF have their best recruitment during "cool" years that have negative values in row 12 of Table 1.

Sections two and three of this report are intended to explain and give additional background on the physical and biological data series used in Table 1. Sections four and five expand and discuss the results given by Table 1.

2. Biological Data Series

A zooplankton abundance data series is presented with the widow and chilipepper RF recruitment time series to allow consideration of the young-of-the-year rockfishes' biological environment. All biological systems are affected by physical environmental changes. Comparison of the three series (rows 1,7 and 11 in Table 1) supports this.

Widow rockfish (S. entomelas). Widow RF recruitment data (row 1, Table 1) were obtained from the cohort analysis of the 1980 - 1985 catch-age composition data from commercial fishery sampling in Washington, Oregon and California (Hightower and Lenarz 1986). These are summarized in Figure 1. Greatest population recruitment was in 1968 and 1970. The recruitment level shown for 1971 and 1969 may be overestimated because of imprecision in aging 10 and 12 year old fish, i.e. peak spreading. Widow RF are a component of the recreational fishery as far south as Santa Barbara (Love 1981), but the peak commercial catch has been off Oregon with only occasional commercial catch south of San Francisco.

Since 1978 widow RF have become the object of a targeted single species fishery. Unlike fishing methods for other RF species (e.g. chilipepper), which are by daytime bottom trawl, the adult widow RF are more vulnerable to nighttime mid-water trawling. Dense vertically-oriented schools form at night and disperse at dawn, when widow RF become incidental in the daytime bottom trawl fishery (Wilkins 1986). The dense single species aggregations were discovered in 1978. By 1980 annual harvest increased 20 fold to 21 thousand metric tons. The "boom" years of 1980 through 1983 were sustained by the highly successful 1968 and 1970 year classes. As these cohorts were exhausted in the absence of succeeding good year classes, the fishery

Table 1. Comparison of sequences of annual values for widow and chilipepper rockfish recruitment (rows 1 and 11), indicators of the physical environment (rows 2, 3, 4, 5, 7, 8, 9, 10) and a composite physical parameter derived by adding rows 3, 4, 5, 6, 8, 9 and 10 (row 12). Years from 1965 to 1980 are entered across the top. Row designations as follows: row 1(Widow RF), widow rockfish recruitment time series; row 2(EN/AL), occurrence of California Current warming event types, EN = El Nino and AL = Aleutian Low induced coastal warming; row 3(1st dif. 25m T), large scale coastal (32 - 50 degrees north) first difference winter temperature anomaly at 25m; row 4(AL index), Aleutian Low atmospheric pressure indicator, "+" means greater development; row 5(B. C. SST), British Columbia Sea Surface Temperature (SST); row 6(N. Transport) index of tendency to anomalous northward transport in the California Current; row 7 (Zooplank.), zooplankton abundance indicator; row 8(Downwelling), winter coastal downwelling indicator at 42 degrees north; row 9(Cen. Cal. SST), composite central California SST indicator; row 10(SF Sea Level), San Francisco sea level height anomaly; row 11(CP RF), relative chilipepper rockfish recruitment; row 12 (Sum), composite physical parameter. In the biological time series, capital letters mean largest values with the asterisks indicating maxima. Lower case letters (w, z, c) indicate above average values. The "0," "x" and "n" symbols are for average and low values and no data respectively. Blank means data inconclusive (row 11). Numerical values for physical parameters were divided into three bins: "+" above average, "0" for average, "-" below average, "++" and "--" indicate extremes. Split symbols, e. g. "+/-", mean above the mean for at least 3 months at the start of the year, remainder "-". Note that the winter events or values shown in rows 2, 3, 4 and 8 that take place in two calendar years are placed in the second calendar year. Widow rockfish (row 1) have most successful recruitment during "warm" years which have "+" values in row 12. Chilipepper rockfish appear to have better recruitment during "cool" years which have "-" values in row 12.

Year	1965	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Widow RF						*										
(1)	n	n	n	w	w	w	w	x	x	x	x	x	0	w	x	w
EN/AL				AL		AL							AL	AL		
(2)	EN	EN	AL			EN	EN						EN (en)	AL		
1st dif.																
25m T (3)	=	+	0	+	-	+	=	-	+	-	+	-	++	-	-	++
AL Index																
(4)	=	-	0	++	-	++	+	-	0	-	-	=	+	++	-	++
B.C. SST																
(5)	0	+ / 0	+	+ / -	-	+ / -	=	=	+ / -	0	-	-	+ / 0	++	0	++
N.Trans-																
port (6)	- / +	+	+	0	+	+ / n	-	- / +	+ / -	-	=	- / +	+	++	+ / n	n
Zoo-									*						*	
plank. (7)	z	z	z	z	0	0 / z	z	z / x	x	0	0	n	n	x	x	n
Downwell-																
ing (8)	-	-	-	-	0	++	-	=	-	-	-	=	-	++	=	++
Can. Cal.																
SST (9)	- / +	+	+	+	+	+	0	+	+ / -	-	=	- / +	+	+ / -	0 / +	+ /
SF Sea																
Level (10)	0	0	0	+	++	+ / -	=	-	+	-	-	=	- / +	+	0 / +	+
Cp RF										*						
(11)	c				c		c	x	c	c	c	0	x	x	c	n
Sum																
(12)	-5	+2	+2	+4	+1	+7	-7	-6	+1	-6	-7	-8	+5	+8	-1	+9

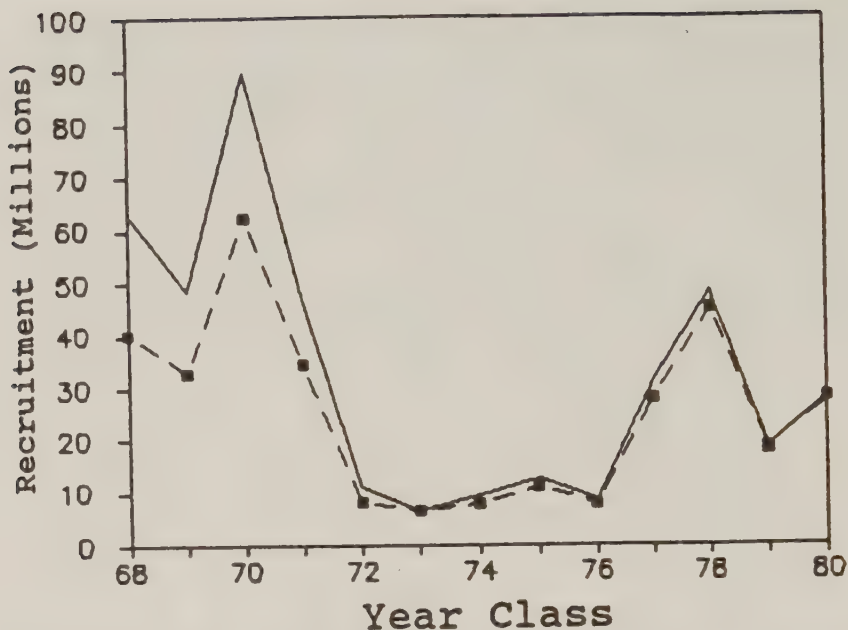


Figure 1. Cohort analysis estimates of widow rockfish recruitment at age 5 for the 1968 - 1980 year classes. Instantaneous rate of natural mortality was set at 0.15 (broken line) and 0.20 (solid line). The last three year classes may not be fully recruited to the fishery. Analysis and table from Hightower and Lenarz (1986).

slumped (Wilkins 1986, Gunderson 1984). Figure 1 shows poor widow RF recruitment for five consecutive years from 1972 through 1976. These were cool California Current years with mild winters (Table 1, rows 4, 5, 8). The 1976-1977 winter brought a climatic shift to conditions that were again favorable to widow RF recruitment.

Chilipepper rockfish (*S. goodei*). Chilipepper rockfish has commercial importance mainly in central California. Annual catch is 2,000 metric tons, all south of the northern California border. Except for zonal distribution, its ecology and also its morphology appear similar to Pacific ocean perch (*S. alutus*) (Adams 1980). Catch-age composition data submitted to the Pacific Fisheries Management Council by Henry (1986) are summarized in Table 2. Table 2 was abstracted to give row 11 of table 1. Table 2 lists the eight most important cohorts contributing to the total California commercial trawl catch between 1978 and 1983. Each column lists year classes in descending importance to the total catch. The number in parentheses is the number of thousands of fish in the most numerous cohort. Relative abundance of the seven other most important cohorts is indicated as percent of the most abundant contributor.

Table 2. Summary of the chilipepper catch-age data for 1978 - 1983. The eight most important year classes contributing to the total California commercial trawl catch are listed for each year. Each column lists year classes in descending importance to the total catch. The number in parentheses is the number of thousands of fish in the most numerous cohort sampled by the commercial fishery. Relative abundance of the seven other most important cohorts is indicated as percent of the most abundant contributor. For the entire series, the major contributing cohorts in descending order are given in column 7.

Year	1978			1979			1980			1981			1982			1983			Total	
	Rank	Yr	%	Rank	Yr	%	Rank	Yr	%	Rank	Yr	%	Rank	Yr	%	Rank	Yr	%	Yr	%
1		69	(230)	73	(540)	75	(750)	75	(630)	75	(630)	73	(330)	73	(330)	71	(400)	75	(2536)	
2		73	80	75	74	74	68	73	70	75	94	75	94	75	98	73	84			
3		71	78	71	43	73	55	74	60	74	72	73	72	73	60	74	61			
4		70	62	72	43	72	49	72	27	71	45	79	40	71	54					
5		68	57	76	43	71	35	76	27	76	39	76	38	76	36					
6		72	55	74	33	76	31	71	25	72	21	74	35	70	28					
7		67	39	70	32	69	20	70	21	79	18	77	23	69	26					
8		74	39	68	26	70	17	77	10	70	18	70	18	68	16					

An average or better year class will enter the list of eight most numerous year classes in its third, fourth or fifth year. It will be found in the four most abundant year classes for three or more years (e.g. 1974). Finally, the cohort will drop from the list of most numerous year classes as its numbers are depleted by fishing (e.g. 1972). Relative year class strength can be estimated from the time dependent ranking of cohorts and the persistence of its residence among the top catch contributors (Table 2). The results of quantitative catch-at-age analyses (Deriso et al. 1985) are comparable to the results developed below (Henry 1987).

For the entire series, the major contributing cohorts in descending order are: 1975, 1973, 1974, 1971, 1976, 1970, 1969, 1968 (column 7, Table 2). The 1975 year class became the second most important cohort in its fourth year and remained a top contributor for the entire period. This was an unusually successful recruitment year and was the most abundant year class in the record high landings of 1980. The 1973 cohort was not sampled until its sixth year, but its place as second overall suggests that it also was an unusually abundant cohort. The 1974 year class was optimally sampled by the 1978 through 1983 period and there is probably some spreading of the 1973 and 1975 modes into 1974 because of aging imprecision. There is insufficient information to conclude that the 1974 period was much better than a high average year in terms of recruitment. The 1971 cohort appears strong in that it was a major contributor to the fishery throughout the period even though it was not sampled until its eighth year. The increase in importance of the 1971 cohort from sixth in 1981 to first in 1983 may be the result of deeper trawling necessitated by the 1982-83 El Nino conditions. The 1976 cohort became important in its third year, but its ranking in the catch has always been lower than fourth. Aging imprecision probably lead to the overestimation of this year class because of its proximity to the very strong 1975 year class. There may have been a moderately good year class in the 1968 - 1970 period, possibly 1969. The cohorts of 1972, 1977 and 1978 are weak, in this order of decreasing abundance. The 1979 cohort is unusually numerous compared to the two predecessors (Henry 1986). It was seventh in importance in its third year and fourth the following year (Table 2).

Results of fishery-independent trawl surveys by the Northwest and Alaska Fishery Center/NMFS suggest that the 1965, 1969, 1974 and 1975 chilipepper RF year classes have been more successful than average (Coleman 1986). This is in general agreement with the results presented by Henry (1986) and has been used to complete the 1965-70 section of the chilipepper recruitment time series.

Zooplankton abundance. Continental shelf rockfish are known to feed on zooplankton (Brodeur and Pearcy 1984). Overall zooplankton abundance in the California Current south of San Francisco as given by Chelton et al. (1982) is

summarized in row 7 of Table 1. The years thought to be most successful for both widow and chilipepper RF were average zooplankton years. This may represent a balance in caloric competition at the planktonic level. That is, a balance between having low enough planktonic predation to survive and having high enough planktonic food to grow may be important in rockfish planktonic stages. The zooplankton index is not included in the combined physical parameter (Table 1, row 12).

3. Physical Parameters

The physical parameters used in this study were chosen for completeness in the 1965 - 1980 period, for possible generality in reflecting physical conditions in areas of greatest chilipepper and widow RF abundance, and for general availability. The following subsections will give additional detail on the abstracting and binning of the physical data sets used in Table 1. Table 1 row headings are included with the subsection headings.

California Current Warming Events(EN/AL). Although the Sebastes environment in the California Current region is over the continental shelf and slope, the forces that affect this environment may originate thousands of kilometers distant in the tropical and north Pacific (Quinn 1978, Uda 1962, Norton et al. 1985, Mysak 1986). Row 2 in Table 1 indicates the occurrence of two warming event types (EN = El Nino, AL = Aleutian Low Intensification). The observed coastal impacts of the El Nino and Aleutian Low warming occur in fall and winter thus extending over two calendar years (Breaker and Mooers 1987), e.g. 1972-73 or 1976-77. In Table 1 the notation for these events are placed in the second year, 1973 and 1977 respectively.

The California Current System (CC) is a broad eastern boundary system of weak but persistent north to south surface flow off the west coast of the United States (Hickey 1979). The CC inner boundary is the coast and the outer boundary is a broad transition zone 3-400 km offshore. The origins of two California current warming event types are diagramed in Figure 2. El Nino effects are carried into the CC region from the tropics by poleward traveling coastally trapped downwelling wave packets which depress the thermocline and cause coastal warming. (Huyer and Smith 1985, Chelton and Davis 1982, Enfield and Allen 1980, Picaut 1985, Mysak 1986). These El Nino perturbations that originate as equatorially trapped Kelvin waves (Cane 1983) are denoted by the solid arrows in Figure 2. Coastal bathymetric and bathythermal irregularities cause the eastern boundary trapped waves to leak energy to the west as downwelling baroclinic Rossby waves. (Rienecker and Mooers 1986, Mysak 1986)

The second warming event type is associated with an intensification of the Aleutian Low Pressure System and its counterclockwise circulation (around "L" in Figure 2).

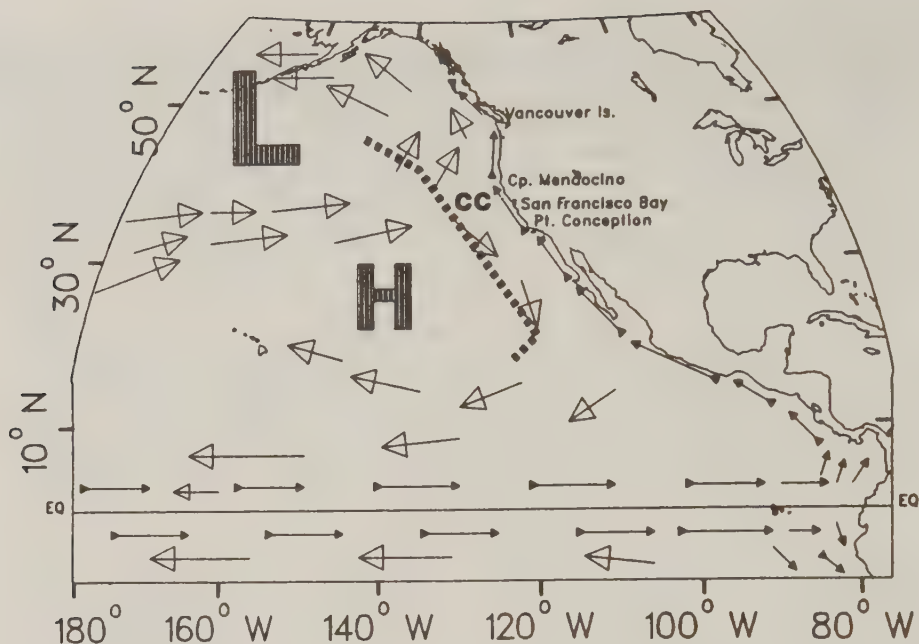


Figure 2. Origins of two California Current (CC) warm event types. The outer boundary of the CC transition zone is indicated by the dotted line. El Nino effects are brought to the CC region by poleward traveling coastally trapped waves originating as equatorially trapped Kelvin waves (small solid arrows). Intensification of the Aleutian Low atmospheric pressure system (block L) affects the CC throughout its range by intensification of winds that oppose its normal flow to the south (open arrows). As the low expands, the eastern limb of the cyclonic circulation brings anomalous south to north winds to the coast which enhance winter downwelling. The atmospheric pressure pattern shown in this diagram is representative of the early March mean.

Intensification of the Aleutian Low pressure system is a deepening or increasing magnitude of negative pressure anomalies in the lower atmosphere (Wallace and Gutzler 1981). This has effects throughout the north Pacific. The California Current is affected throughout its range by anomalous winds that oppose its normal flow to the south. As the Low expands, the eastern limb of the cyclonic circulation brings south to north winds along the coast. Then local and remote wind forcing combine to augment processes that depress the thermocline in the California Current and warm the coastal ocean, but this effect is usually limited to the upper 150m (Norton et al. 1985, 1987).

There is a tendency for deep Aleutian lows to develop during El Nino years when there is extensive equatorial warming as in the winters of 1969-1970 and 1976-1977 (Wallace and Gutzler 1981), but sometimes the low does not intensify even when there is extensive equatorial warming as in 1965 and 1972 (Douglas et al. 1982). The Aleutian Low may also intensify without apparent tropical warming as in 1967-1968 and 1979-1980 (Norton et al. 1985).

Patterns of dependence among physical parameters. Patterns of dependence among physical parameters are shown in Table 3. This table shows the association tendency among the physical parameters discussed in this study. The three interannual event types distinguished in this paper are shown. During an El Nino year (Table 3, col. 1), the warming effect on the California Current (CC) may be called the "California El Nino." During the California El Nino the sea level height and northward transport anomalies increase (Huyer and Smith 1985). Along parts of the coast there is northward surface flow as a persistent year-round feature (Bird et al. 1984, Hickey 1979.)

The Aleutian Low Index (AL Index in Table 1) may be above or below average during a California El Nino and coastal downwelling may be above or below average (Tables 1 and 3). Since the California El Nino brings warm water into the coastal zone, the north to south flow tendency of the CC is decreased. During Aleutian Low warming (Table 3, col. 2), the Aleutian Low index will increase indicating intensification of the north Pacific Low pressure system. Unusually strong coastal downwelling is common during an Aleutian Low warming. Other effects will be similar to those of the California El Nino. One of the several definite relationships shown in Table 3, is the connection between winter downwelling (row 3), onshore transport of surface water and increased transport to the north. If coastal wind stress is from south to north along the coast, surface water will be transported onshore (row 6) and downwelling will occur. As an adjustment to redistribution of water, northward flow will be increased (row 5). Increased northward flow is the result of onshore flow, which may result from California El Nino, Aleutian Low or local forcing. Onshore flow may be important in producing conditions leading to increased widow RF first year survival. During the CC cool event (Table 3, col. 3), all the parameters will tend to reverse (become "-") in value except transport to the south, which will increase. Onshore transport usually brings warmer water to the coast. Consequently, SST (row 1) and sea level (row 4) will be increased. Table 3 represents an idealized view of the relationships among physical parameters presented in Table 1.

The relationships among the physical parameters involve the change from one point to another on a functional surface which results in increased or decreased variable value. Many combinations of binned variable

Table 3. Idealized representation of three California Current Interannual Events (columns) in terms of common parameter anomalies (measurements). The rows are: Sea Temperature, row 1; Aleutian Low index, row 2; winter downwelling, row 3; Sea Level height anomaly, row 4; Northward Transport tendency, row 5; Onshore Transport, row 6 and CC southward flow. The warming events will have positive anomaly measurements except for California Current transport to the south which will be reduced. Anomalies will have reverse tendency during cool events (col. 3). The "+/-" entries reflect opposite possibilities. The California El Nino may occur with or without Aleutian Low induced warming (row 2) and enhanced winter downwelling may or may not occur during Aleutian Low warming events (row 3).

Event	>	California El Nino	Aleutian Low	California Current
Measurement		warming	warming	cool event
Sea Temp.	(1)	+	+	-
AL Index	(2)	+/-	+	-
Downwelling	(3)	+/-	+/-	-
Sea Level	(4)	+	+	-
N. Transport	(5)	+	+	-
Onshore Trans.	(6)	+	+	-
Cal. Cur.	(7)	-	-	+

values are possible in a given event type, even when scaled to long term means (Table 1). Observed combinations will depend on the event intensity and the state of the CC and north Pacific atmosphere when the signals arrive. For instance, the 1972-73 El Nino was intense in the tropics, but an intensified Aleutian Low did not develop, and northward flow tendency increased during the 1972-1973 winter. Then flow shifted strongly to the south in late 1973 (Chelton et al. 1982, Huyer et al. 1978).

First difference 25 meter temperature (1st dif. 25m T). The first difference of the standardized temperature anomaly at 25 meters depth for a 200 km wide coastal strip extending from 30 to 50 degrees north latitude is shown in row 3 of Table 1. Data in this area were also averaged for a period from October through March (Norton et al. 1987). The year designation is the same as for the associated January. First differences are the average standardized temperature anomaly for a given year minus the value from the preceding year. This procedure emphasizes interannual change. A "+" entry means the current year is warmer than the preceding year and "++" ("=") means that the warming was maximum (minimum) or within 10% of the maximum (minimum) value. Note that the first difference coastwide standardized anomaly is positive for every warming event in the 1965-80 series (Table 1). That is, each of the "EN" and "AL" years produced a signal in the coastwide anomaly that indicates warming over the preceding year (Table 1, rows 2 and 3).

Aleutian Low (AL Index). Aleutian Low Intensification (Table 1, row 4) was measured directly by the negative mean monthly anomaly of the 500 millibar atmospheric height at 45 degrees north latitude by 165 west longitude ("L" in figure 2). The sign of the anomaly is reversed and bins assigned according to the conventions of Wallace and Gutzler (1981). A "+" notation in row 4 indicates intensification of the Aleutian Low Pressure System over the mean. The "++" notation indicates a particularly intense Aleutian Low. The "0" means average Aleutian Low development. An Aleutian Low that is more intense than average will also be larger than average. As it expands, the Eastern Pacific High is shifted southward and winds from the south become more common over the CC System (Figure 2). The deepest Aleutian Lows were coincident with the best years for widow RF recruitment.

British Columbia Sea Surface Temperature (B. C. SST). British Columbia SST (row 5 in Table 1) was derived from monthly mean temperature anomalies (from a 30 year monthly mean) at Race Rocks on the southern tip of Vancouver Island (Tabata 1985). Symbols were assigned to divide the data into three bins as follows: "+," anomaly greater than +.25 degree Celsius; "0" for anomalies of absolute (unsigned) value less than .25; "++" and "=" indicate extreme values. In some cases it was not possible to unambiguously state that the entire year was above or below average. So, "+/-" means that the first part of the year (at least three months) was above average temperature and the last part of the year (at least three months) was below average temperature. Note that "-" values typical of the 1971 - 1976 period correspond to the best recruitment years for chilipepper RF.

Northward California Current Transport (N. Transport). An integrated index of northward CC flow (row 6, Table 1) in an area 200-400 kilometers from shore extending from 26 to 38 degrees north is extracted from Chelton et al. (1982). The symbols "+" and "n" mean northward transport and no data respectively. Fortunately, this unique time series is nearly complete in the 1965 to 1980 interval of interest. Although its exact meaning might be subject to considerable interpretation, agreement in independent measurements over the continental shelf and slope (Huyer et al. 1978, McLain and Thomas 1983, McLain et al. 1985) suggest that this transport tendency index has some applicability in assessing the rockfishes' environment. In general it appears that, northward transport has favored widow RF recruitment and southward transport has favored chilipepper RF recruitment.

Winter Season Downwelling Index (Downwelling). An annual index of coastal downwelling (row 8, Table 1) during the winter season at 42 degrees north was derived by Norton et al. (1985) by accumulating the monthly mean upwelling

index values of Bakun (1973) and reversing the sign. The convention of plus and minus symbols is similar to the parameters already discussed. In terms of percent of the highest value, the bins were assigned as follows: 0-25%, "=", 25-60%, "-," 60-80%, "0," 80-95%, "+," 95-100%, "++." The numerical average value was at about 68% of the maximum value. The three extreme downwelling years, 1970, 1978 and 1980 were favorable to widow RF recruitment.

Central California Sea Surface Temperature (Cen. Cal. SST)

The central California SST indicator (row 9 of Table 1) was derived from monthly mean anomalies at the Southeast Farallon Islands, 46 km west of San Francisco and at Pacific Grove at the southern end of Monterey Bay 100 km south of San Francisco (Anon. 1981). These two stations represent different coastal environments and the combined data is presented as a temperature indicator closely associated with the chilipepper environment. Combination of the data allowed a complete data set to be derived from two nearly complete data sets. Binning conventions are generally the same as for British Columbia sea surface temperature (above). The most extremely negative value in 1975 corresponds to the most successful (known) chilipepper year class, but this relationship does not appear to hold for all other chilipepper year classes.

San Francisco Sea Level (SF Sea Level). The detrended San Francisco sea level was adapted from McLain (1983) for row 10 of Table 1. Sea level anomaly is an indicator of coastal current tendencies and integrated sea temperature (higher sea level anomaly suggests more northward flow and higher integrated temperature anomaly of the water column) (Chelton and Davis 1982, Norton et al. 1985). The division of the anomaly range into three bins and extremes was based on taking the range of anomalies less than 5 cm absolute value as average or "0." Extremes and anomalies within 10% of the extremes are given "++" and "=" symbols. In several cases, negative anomaly corresponds to good chilipepper RF first year survival and positive anomaly appeared to favor enhanced widow RF first year survival. The role of sea level extremes does not imply a direct relationship between sea level at San Francisco and rockfish recruitment.

4. Results

The individual measurements of the physical environment have been combined in a simple straightforward way by first dividing the data series values into three categories or bins to show patterns. Then the binned values were added together to give an overall representation of the pattern. The result of this process is given in row 12 of Table 1. This combined parameter was then compared to the recruitment data for widow and chilipepper rockfish (table 1, rows 1 and 11). The major results of these pattern comparisons are listed below.

1. Different physical conditions are required for optimum widow and chilipepper RF recruitment. Certain intermediate years, in terms of the combined physical parameter (Table 1, row 12), may support moderate recruitment in both species.

2. Widow RF recruitment is favored by winters with deep Aleutian Lows, violent winter storms on the coast, above average sea temperatures, enhanced northward flow in the the California Current and anomalously high coastal sea level. Widow RF recruitment seems to be facilitated by the common large scale warming events (Table 1, row 2). However an El Nino alone, unaccompanied by anomalously deep Aleutian Low development as in 1966 and 1973, does not appear to favor enhanced widow RF recruitment. The Aleutian Lows that expand over the coast and bring frequent winter storms with strong winds from the south to intensify coastal downwelling seem more important than the Californai El Nino in enhancing widow RF recruitment (Table 1).

3. Chilipepper RF fish recruitment appears to be facilitated by cool water, and increased southerly CC flow conditions as described ideally in table 3, column 3, or more realistically in table 1 under 1971 and 1975. Exceptionally good chilipepper recruitment does not occur in years of exceptionally good widow RF recruitment.

4. The coastal ocean from central California to Vancouver Island has undergone three climatic shifts in the 1965 - 1980 period. First, there was a warm period of five years which included two California El Ninos and two Aleutian Low events. In 1970 the two warm event types combined to create conditions that appeared exceptionally favorable to widow RF recruitment. After 1970 a shift to an ocean climate of cool sea temperatures and increased southerly flow in the CC occurred. This cool period lasted until 1976 and included all the most numerous chilipepper RF cohorts contributing to the 1978 to 1983 catch. In 1976 the ocean climate shifted back to the warmer regime. Again young-of-the-year widow RF survival appears to have been enhanced as CC warming events became more frequent.

The catch-age composition data suggest that 1969 and 1971 were moderately good recruitment years for widow RF. These were also at least moderately good years for chilipepper RF recruitment. It is probable that because the very successful 1968 and 1970 widow RF cohorts were not aged until they were over ten years old, there is some peak spreading due to aging imprecision. The 1969 year class would be most likely to be overestimated if aging imprecision is Gaussian, since it is between the two most numerous cohorts. However, if it is more likely that

annular otolith rings will be missed more frequently than erroneously added, then the 1971 year class would be the most likely to be overestimated because it follows the most numerous cohort. The 1969 year class will be second most likely to be overestimated. Combining this reasoning about aging imprecision with the findings that chilipepper RF recruitment is facilitated during cool events (Table 3), can lead to the not unreasonable conclusion that the apparent ambiguity in recruitment data for 1971 is the result of overestimation of the size of the 1971 widow RF cohort. The physical environment of 1971 appears favorable to chilipepper RF recruitment (Table 1).

Environmentally, 1969 and 1971 were very different. If better than average recruitment was to occur in both chilipepper and widow RF in the same year, it would be expected to occur in a year such as 1969 when the sum of physical parameters is not conspicuously in the minus or plus domain. The catch-age composition data for chilipepper RF does not give definite information about the strength of this year class compared to the strong year classes of the 1970s. It is likely that the 1969 widow RF year class was also overestimated, but the extreme positive sea level anomaly suggests that this year was more favorable to enhanced widow RF recruitment. High coastal sea level is consistent with increased northward flow along the coast. This is confirmed by the northward flow index (Table 1, rows 6 and 10). Increased northward flow may be the factor in common with Aleutian Low warming events that facilitate widow RF recruitment (Table 3). Chilipepper RF recruitment may have been enhanced in 1969 relative to 1968 and 1970 and may have been poor compared to 1973 and 1975.

Results of the Northwest and Alaska Fishery Center's 1980 Bottom Trawl Survey show that the 1965 chilipepper RF cohort was especially numerous (Coleman 1986). This is consistent with the relationships which are also evident during the 1971 - 75 period (Table 1).

The 1972 year class is conspicuously weak in the chilipepper catch-age composition data of Henry (1986), but the environmental data appears favorable to a strong chilipepper year class. The inshore CC was affected by the 1972-73 El Nino in the spring of 1972 (Enfield and Allen 1980, Chelton and Davis 1982, Huyer and Smith 1985) and this may have had an impact not reflected in the physical parameters presented. Likewise the 1976-77 El Nino may have curbed survival of the 1976 year class of chilipepper RF. The 1965 and 1969 chilipepper year classes, however, appear as though they may be exceptions to the reasoning just used to explain poor recruitment in 1972 and 1976.

5. Discussion

The combined physical parameter developed above gives a numerical value to the ideal California Current event types : Aleutian Low induced warming, California El Nino

coastal warming and California Current cool events (Table 3). The larger unsigned values belong to years with warm or cool events undiluted by opposite event types (Table 1). The best years for chilipepper and widow rockfish recruitment occur when the value of combined parameter is at or near its maximum unsigned value. Negative anomalies favor recruitment in chilipepper rockfish, while positive anomalies favor widow rockfish recruitment (Table 1). This result, suggests that the present approach may be appropriate, but it does not necessarily mean that the most important physical terms have been included in the analysis. Future research must be sensitive to other parameters' ability to match patterns of fish stock recruitment and add dimension to descriptions of the fishes' environment.

The simple system used here allows some knowledge of the biological systems to be gained without knowing exactly how the biological systems are affected by the physical environment or even what particular aspect of the physical environment is most important. Also, the assumption that the biological system is reacting in a simple straightforward way need not be abandoned. The assumption that can be avoided in using the multidimensional approach is that the rockfish systems react directly to physical parameters as we happen to measure them, e.g. temperature, sea level, etc.

Species distinction has been shown to be important. If, for instance, recruitment of chilipepper and widow RF were summed, it would be much more difficult to form associations with physical environmental patterns. Another species distinction is that the value a particular physical data set will have in helping to understand recruitment will depend on the species involved. The data presented in table 1 are somewhat more successful in describing the widow RF recruitment data set than in describing the chilipepper recruitment data set. Widow RF recruit best under the Aleutian low, El Nino and downwelling conditions. The only apparent exception is 1971, the year following the most numerous year class in the record. This may not be an exception because 1971 is the year class most likely to have its size overestimated because of the tendency to miss annular rings in aging older fish.

Figure 3 summarizes some of the points made above. It is a scale-less grid or coordinate system with two main axes. The vertical axis represents advective current flow in the CC system. Increased northward flow is toward the top of Figure 3, while increased flow to the south is represented by the space below the horizontal axis. Negative atmospheric pressure anomaly or an intensified Aleutian Low Pressure System is toward the right on the horizontal axis. Positive anomaly representing a less developed Aleutian Low is to the left. The right side of the horizontal axis is further divided into two areas. When the winter-time Aleutian Low extends over the coastal

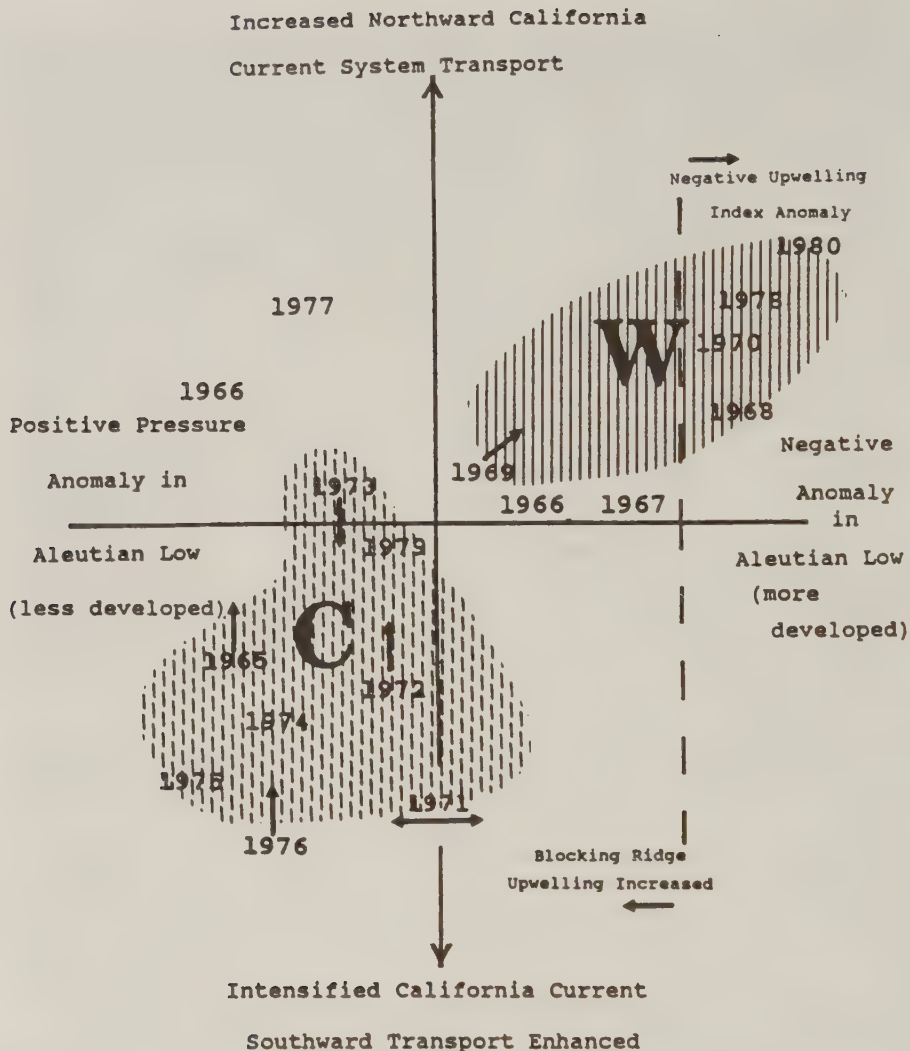


Figure 3. Coordinate system organizing rockfish recruitment data and physical parameter tendencies into four quadrants. The vertical axis represents advective current flow in the CC system. Increased northward flow is toward the top and increased southward flow is represented by the space below the horizontal axis. Negative atmospheric pressure anomaly in an intensified Aleutian Low is to the right. The positioning of the year designations was done on the basis of the combined parameter (table 1, row 12). Arrows associated with the date give inferred direction of change during the year. Years that favor chilipepper rockfish are in the lower left quadrant (broken hatching) and years that favor widow rockfish recruitment are in the upper right quadrant (solid hatching).

When the winter-time Aleutian Low extends over the coastal California Current System, it frequently results in increased winter downwelling (Figure 3, right of dotted line). The area in the upper right quadrant between the main vertical axis and the dotted vertical ancillary axis would contain years when the Aleutian Low did develop but was blocked from the coast by a high pressure ridge as in the 1976-1977 winter (1977 in Table 1). The 1967 - 1968, 1977 - 1978 and 1979 - 1980 winters (1968, 1978 and 1980 respectively in Table 1) would be to the right of dotted line in the upper right quadrant. The upper left quadrant is the area of California El Ninos that occur without Aleutian Low intensification. El Nino years of 1966 and early 1973 would be in this quadrant. Columns 1 and 2 in Table 3 would represent the area above the horizontal axis in the left and right quadrants respectively. If the event types occurred together in a combined event as in 1969 - 1970, the year would be placed in the upper right quadrant. The high downwelling value for 1970 moves the year further to the right past the dotted line. These years are usually warm with elevated coastal sea level and increased onshore transport in the coastal ocean's surface layers (table 3).

The space below the horizontal axis in Figure 3 corresponds to the cool CC years when transport to the south is enhanced. (table 3, col. 3). The lower left quadrant would contain the cool years of the early and mid-1970's. Aleutian Low enhancement is not as frequent or intense during cool periods, so few years will be characteristic of the lower right quadrant. In the 1965-80 series, 1971 is a possible example. The lower left quadrant contains 1965(early), 1972(early), 1973(late), 1974, 1975, 1976(early), and 1979 which were definitely cool and largely devoid of warming event influence as these influences are described in this study.

Years that appear to favor chilipepper recruitment are in the lower left quadrant and those that favor widow rockfish recruitment are in the upper right quadrant of Figure 3. The best widow rockfish years are to the right of the dotted line indicating that the best widow rockfish recruitment years have intense coastal winds which bring warming of the surface layers of the coastal ocean and leading to northward transport. Increased onshore, cross shelf, transport will accompany increased northward transport. This will carry pelagic larvae and weakly swimming early juvenile stages toward shore.

This possible mechanism for increased widow RF recruitment fits the generalities proposed by Parrish et al. (1981) that explain fish species distributions along the Washington, Oregon and California coasts. They state that the California Coast between Cape Mendocino and Point Conception is unfavorable to recruitment of species with pelagic eggs and larvae because of the vigorous surface offshore transport that accompanies the nearly year around upwelling circulation (Parrish et

al. 1981, Bakun and Parrish 1980). At present there is no way of knowing if onshore transport is the important environmental factor in widow RF recruitment, but the data suggest an important winter mechanism that has dynamics in common with northward and onshore CC System transport. If widow RF depend on winter onshore transport to maintain early life stages in favorable environments for settling and the onshore transport is wind driven (apparently the more the better, table 1), then it is not surprising that the commercial fishery for widow RF does not extend south of San Francisco, and that the targeted fishery of the early 1970s was centered off Oregon where winter winds from the seasonally intensified Aleutian Low are a conspicuous feature of the mean annual cycle. It may be that the prolonged upwelling season and associated offshore transport, or divergent flow, characteristic of the central California Coast carries planktonic stages of widow RF larvae offshore into environments hostile to survival and growth. If planktonic stages of widow RF are characteristically in the surface layers, then it is probable that this is the mechanism inhibiting population maintenance off central California.

It is clear the chilipepper rockfish which have maximum abundance on the central California coast are dependent on different conditions than those favoring excellent widow rockfish recruitment. Chilipepper rockfish recruitment is favored by cool years, but the fact that there was good recruitment in 1973 suggests that the cool conditions of the later part of 1973 were more important to young-of-the-year survival than that year's warm initial months. That is, the later part of 1973 appears to fit the pattern that would favor chilipepper RF recruitment. It may be that the character of the winter months at the beginning of the chilipepper rockfishes' first year is less important in determining chilipepper RF survival than they appear to be in determining widow RF survival. The fact that chilipepper rockfish are most successful on the central California coast suggests that they have specific adaptations in their early life history that allow them to avoid being swept offshore in larval and planktonic juvenile stages by the surface offshore transport that accompanies the characteristic upwelling circulation.

Other rockfish species. Preliminary studies of the kind described above are being conducted on yellowtail (*S. favadus*) and canary (*S. pinniger*) rockfish. Data from the 1960-70 period, suggest that yellowtail rockfish recruit better during El Nino years. Years with and without intensified Aleutian Low development may be equally favorable. This would place yellowtail RF in the upper two quadrants of Figure 3 indicating that their recruitment is enhanced by any event forcing northward CC flow. Canary rockfish appear to have better recruitment when there is more southward transport. So, the years favoring canary rockfish recruitment would fall below the horizontal axis in Figure 3. More definite conclusions regarding these

species will have to await more complete and accurate recruitment time series.

Fisheries management and investment planning. Understanding the probabilistic nature of recruitment periodicity is essential to resource managers as well as investors looking for maximum return on their investment. Knowing the climatic regime that favors or inhibits recruitment in a targeted species, could lead to better knowledge of how sustainable a fishery might be and what limitations on exploitation may be necessary to maintain a sufficient stock of adults to take advantage of good recruitment conditions when they occur.

Since several time series of physical parameters exist of five to ten decades length, it may be possible to treat these as proxy-variables of recruitment and get quantitative information on expected variability in recruitment.

Widow rockfish boom and bust. The knowledge of the spectacularly good widow rockfish recruitment of 1968 and 1970 followed by very poor recruitment from 1972 through 1976 suggests an explanation for the boom and bust history of the targeted widow RF fishery (Gunderson 1984). It is possible that the discovery of the midwater widow RF fishery in the late 70's was the result of the excellent recruitment conditions of 1968 and 1970. Suddenly, eight years later, there was a large exploitable biomass of widow rockfish which had not been noticed before because it was not there. After the abundant widow rockfish resource was discovered, the fishery increased twentyfold in two years based on the unusually good 1968 and 1970 year classes. The decline in the fishery that began in 1982 was the result of depletion of the two strong year classes. The cool, strong CC years that followed 1970 inhibited widow rockfish recruitment, providing no additional input to the fishery resource in the early 1980's. It will be interesting to note how successful the 1980 widow rockfish year class will be. According to the data presented in table 1, 1980 should be a very good year and initial catch-age composition data suggest that it is a numerous cohort (Figure 1). Data at full recruitment are not presently available.

The combined physical and biological data presented in this report suggest that the bio-economic boom to bust event chronicled by Gunderson (1984) for widow rockfish is perfectly natural considering the pulsed recruitment common in this species and the climatological background of the event. When more is known of the physical conditions favoring the 1968 and 1970 year classes, it will be possible to analyse the historical records and determine expected frequency of proper conditions for exceptionally good recruitment.

Acknowledgements

The author would like to thank Bill Lenarz of the Southwest Fisheries Center's Tiburón Laboratory (NMFS) and Frank Henry of the California Department of Fish and Game for their patience and instruction concerning the rockfish data used in this report. This manuscript would not have been completed without the help of Rosemary Troian, Marlene Hughes and the many hours of consultation and encouragement received from other members of the Pacific Fisheries Environmental Group.

REFERENCES

- ADAMS, P., 1980. Morphology and distribution patterns of several important species of rockfish (Genus Sebastes) Mar. Fish. Rev., 42(3-4): 80-82
- Anonymous 1981. SIO Reference 81-30
Surface water temperatures at shore stations -
United States west coast. Marine Life Research
Committee and Marine Life Research Group, University
of California, Scripps Institution of Oceanography,
La Jolla, CA, 92037, 45pp.
- BAKUN, A., and R. PARRISH, 1980. Environmental inputs to
fishery population models for eastern boundary
current regions. In Workshop on the effects of
environmental variation on the survival of larval
pelagic fishes. Ed. by G. Sharp. Intergovernmental
Oceanographic Commission, UNESCO, Paris. IOC Workshop
Rep., 28:67-104.
- BAKUN, A., 1973. Coastal upwelling indices, west coast of
North America 1946-1971. NOAA Tech. Rept. NMFS SSRF
671, 103p.
- BIRD, A., R. KOOB, J. WICKHAM and C. MOOERS, 1984.
Hydrographic data from the slope waters off
central California. 26 November 1978 - 26 June
1980., Dep. of Oceanography, Tech. Rep NPS 68-84-010,
Naval Postgraduate School, Monterey, CA 93943.

- BOEHLERT, G. AND M. YOKLAVICH, 1984. Variability in age estimates in Sebastes as a function of methodology, different readers and different laboratories, Calif. Fish and Game, 70(4): 210-224.
- BREAKER, L. AND C. MOOERS, 1987. Oceanic variability off the central California coast, Prog. Oceanog. (in press)
- BRODEUR, R. AND W. PEARCY, 1984. Food habits and dietary overlap of some shelf rockfishes (genus Sebastes) from the northeastern Pacific Ocean. Fish. Bull., U.S., 82(2): 269-293.
- CANE, M., 1983. Oceanographic events during El Nino. Science, 222:1189-1194.
- CHELTON, D. , P. BERNAL and J. MCGOWAN, 1982. Large-scale interannual physical and biological interaction in the California current., J. Mar. Res., 40(4):1095-1125.
- CHELTON, D. and R. DAVIS, 1982. Monthly mean sea-level variability along the west coast of North America. J. Phys. Oceanog., 12:757-784.
- COLEMAN, B., 1986. The 1980 Pacific West Coast Bottom Trawl Survey of groundfish resources: Estimates of distribution, abundance, length and age composition NOAA Technical Memorandum NMFS F/NWC-100. Northwest and Alaska Fisheries Center NMFS/NOAA 7600 Sand Point Way NE, Seattle, WA 98115.
- CUSHING, D., 1973. Recruitment and parent stock in fishes. WSG 73-1. Washington Sea Grant, University of Washington, Seattle WA 98195.
- DARWIN, C. and A. WALLACE, 1858. On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection. Jour. Proc. Linnean Soc., Zoo., Vol 3. Communicated by C. Lyell and J. Hooker July 1, 1858.
- DERISO, R., T. QUINN, P. NEAL, 1985. Catch-age analysis with auxiliary information. Can. J. Aquat. Sci., 42: 815-824.
- DOUGLAS, A., D. CAYAN and J. NAMIAS, 1982. Large-scale changes in North Pacific and North American weather patterns in recent decades. Mon. Wea. Rev., 110:1851-1862.
- ENFIELD, D., and J. ALLEN, 1980. On the structure and dynamics of monthly mean sea level anomalies along the Pacific coast of North and South America. J. Phys. Oceanog., 10(4): 557-578.

- GUNDERSON, D., 1984. The great widow rockfish hunt of 1980-1982. N. Amer. Jour. of Fish. Management, 4: 465-468.
- HENRY, F., 1986. Status of the coastwide chilipepper (Sebastes goodei) fishery. (Document submitted to the Pacific Fisheries Management Council, Portland, Oregon, October 1986). California Department of Fish and Game, 411 Burgess Drive, Menlo Park, CA 94025.
- HENRY, F., 1987. California Department of Fish and Game, 411 Burgess Drive, Menlo Park, CA 94025. (Personal communication)
- HICKEY, B., 1979. The California current system - hypotheses and facts. Prog. Oceanog., 8:191-279.
- HIGHTOWER, J.E. and W. H. LENARZ, 1986. Status of the widow rockfish fishery. (Document submitted to the Pacific Fisheries Management Council, Portland, Oregon, October 1986). Southwest Fisheries Center, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.
- HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research Rapp. P. v. Reun. Cons. Perm. int. Explor. Mer, 20:1-228
- HUNTER, J. 1982. Feeding ecology and predation on marine fish larvae, In Marine Fish Larvae Ed. by R. Lasker, Washington Sea Grant program, University of Washington, Seattle.
- HUYER, A., R. SMITH and E. SOBEY, 1978. Seasonal differences in low-frequency current fluctuations over the Oregon continental shelf. J. Geophys. Res., 83: 5077-5089.
- HUYER, A. and R. SMITH, 1985. The signature of El Nino off Oregon in 1982-83, J. Geophys. Res., 90: 7133-7142.
- KETCHEN, K., 1956. Factors influencing the survival of lemon sole (Parophrys vetulus) in Hecate Strait, British Columbia. J. Fish. Res. Board Can., 13(5): 647-694.
- LOVE, M., 1981. Evidence of movements of some deepwater rockfishes (Scorpaenidae: genus Sebastes) off southern California. Calif. Fish and Game, 67(4): 246-249.
- MOOERS, C. and A. ROBINSON, 1984. Turbulent jets and eddies in the California current and inferred cross-shore transports. Science, 223: 51-51.

- MYSAK, L., 1986. El Nino, interannual variability and fisheries in the northeast Pacific Ocean. Can. J. Fish. Aquat. Sci., 43:464-497.
- McLAIN, D., 1983. Coastal ocean warming in the northeast Pacific, 1976-83. In The influence of ocean conditions on the production of salmonids in the North Pacific, a workshop, Ed. by W. Pearcy, Sea Grant College Program. Rep. ORESU-W-83-001. Oregon State Univ. Newport, P.61-86.
- McLAIN, D. and D. THOMAS, 1983. Year-to-year fluctuations of the California countercurrent and effects on marine organisms. Cal. Coop. Fish Inv. (CalCOFI) Rep., 23:165-181.
- NORTON, J., D. McLAIN, R. BRAINARD, and D. HUSBY, 1985. The 1982-83 El Nino event off Baja and Alta California and its ocean climate context. In El Nino North, Ed. by W. Wooster and D. Fluharty, pp 44-72, Washington Sea Grant Program, University of Washington, Seattle.
- NORTON, J., D. McLAIN, D. HUSBY and R. BRAINARD, 1987. Evidence for downward propagation of coastally trapped wave energy found in analysis of California current warming event. Pacific Fisheries Environmental Group, Southwest Fisheries Center, NMFS/NOAA P.O. Box 831, Monterey, CA 93942 (in prep).
- PARRISH, R., C. Nelson and A. Bakun, 1981. Transport mechanisms and reproductive success of fishes in the California current. Biol. Oceanog., 1(2): 175-203.
- PICAUT, J., 1983. Propagation of the seasonal upwelling in the eastern equatorial Atlantic. J. Phys. Oceanog., 13(1):18-37.
- PICAUT, J. 1985. Major dynamics affecting the eastern tropical Atlantic and Pacific Oceans. Cal. Coop. Ocean. Fish. Inv.(CalCOFI) Rep., 26: 41-50.
- QUINN, W., D. ZOPF, K. SHORT and R. KUO YANG, 1978. Historical trends and statistics of the southern oscillation, El Nino, and Indonesian droughts. Fish. Bull., U.S., 76(3): 663-678.
- REINECKER, M. AND C. MOOERS, 1986. The 1982-1983 El Nino signal of northern California. J. Geophys. Res., 91(C5): 6597-6608.
- TABATA, S., 1985 El Nino effects along and off the Pacific coast of Canada during 1982-83, In El Nino North, Ed. by W. Wooster and D. Fluharty, pp. 85-96, Washington Sea Grant Program, University of Washington, Seattle.

- TEMPLEMAN, W., 1972. Year-class success in some north Atlantic stocks of cod and haddock. Int. Comm. Northw. Atlant. Fish. Spec. Pub. No. 8, pp.223-238.
- UDA, M., 1962. Cyclic correlated occurrence of world-wide anomalous oceanographic phenomena and fisheries condition. J. Oceanogr. Soc. Jpn. 20th Anniv. Vol:368-375.
- WALLACE, J. and D. GUTZLER, 1981. Teleconnections in the geopotential height field during the northern hemisphere winter. Mon. Wea. Rev., 109:784-812.
- WILKINS, M. 1986. Development and evaluation of methodologies for assessing and monitoring the abundance of widow rockfish, Sebastes entomelas. Fish. Bull., U.S. (84) 2: 287-310
- WICKHAM, J., 1975. Observations of the California Counter Current. J. Mar. Res., 33:325-340.

REVISION OF THE SPOTTED DOLPHINS, *STENELLA* SPP.

W. F. PERRIN

Southwest Fisheries Center, National Marine Fisheries Service,
 P.O. Box 271, La Jolla, California 92038

E. D. MITCHELL

Arctic Biological Station, 555 St. Pierre Boulevard,
 Ste. Anne de Bellevue, Quebec, Canada H9X 3R4

J. G. MEAD

Division of Mammals, U.S. National Museum of Natural History,
 Smithsonian Institution, Washington, D.C. 20560

D. K. CALDWELL

M. C. CALDWELL

Marineland, Inc.

Rte. 1 Box 122, St. Augustine, Florida 32086

P. J. H. VAN BREE

Institute of Taxonomic Zoology, University of Amsterdam,
 36 Plantage Kerklaan, Amsterdam 1018 CZ, Netherlands

W. H. DAWBIN

Division of Vertebrate Zoology, Australian Museum,
 College Street, Sydney, N.S.W., Australia 2000

ABSTRACT

The taxonomy of the spotted dolphins has been confused. Two apparent species exist, one endemic to the Atlantic and the other pantropical. They have sharply different color patterns and non-overlapping vertebral counts. However, the holotype specimens for most of the names that have been applied to the spotted dolphins (including *S. attenuata*, *S. frontalis*, *S. plagiodon* and others) are skulls only, with no information on coloration or number of vertebrae. The two species overlap in all skull characters; geographical variation in both is pronounced. We used a discriminant analysis based on tooth counts and three skull measurements (standardized to skull width) to identify the type specimens to the two species. We used other criteria for assignment of nominal species for which holotype specimens do not exist. We propose that *Stenella frontalis* (G. Cuv., 1829) be used for the Atlantic endemic species and *Stenella attenuata* (Gray, 1846) for the pantropical species and here redescribe the species. Proposed common names are Atlantic spotted dolphin and pantropical spotted dolphin. *S. frontalis* now includes *Delphinus froenatus* F. Cuv., 1829, *D. doris* Gray,

1846 and *D. plagiodon* Cope, 1866. *S. attenuata* (a *nomen conservandum*) includes *D. velox* G. Cuv., 1829, *D. pseudodelphis* Wiegmann, ≤ 1840 , *D. brevimanus* Wagner, 1846, *D. microbrachium* Gray, 1850, *D. albirostratus* Peale, 1848, *Steno capensis* Gray, 1865, *Clymene punctatus* Gray, 1866, *Steno consimilis* Malm, 1871 and *Prodelphinus graffmani* Lönnberg, 1934. Unidentifiable to either of the two valid species are *D. dubius* G. Cuv., 1812, *D. pernettensis* de Blainville, 1817 (suppressed), *D. malayanus* Lesson, 1826 and *D. Rappii* Reichenbach, 1845; these must remain *incertae sedis*.

Key words: *Stenella*, dolphins, taxonomy, *Delphinus*, osteology, geographical variation.

The taxonomy of the spotted dolphins has long been confused (True 1889, Fraser 1950, Perrin 1975, Mitchell 1975, Honacki *et al.* 1982). It is generally recognized that at least two species exist in the Atlantic, one pantropical and the other endemic to the Atlantic (Hershkovitz 1966, Caldwell, Caldwell, Rathjen and Sullivan 1971, Perrin 1975, Perrin *et al.* 1978, Honacki *et al.* 1982). These have been distinguished primarily on the basis of differing color patterns (Fig. 1; Perrin 1975; Leatherwood *et al.* 1983). The nomenclature of these apparent species has been unsettled because the holotype specimens of the several nominal species are skulls associated with no information on the external appearance of the animals in life. In addition, there is pronounced geographical variation in the skulls of both species (described below), leading to the confusing situation of markedly different skulls belonging to the same species in some cases and very similar skulls belonging to different species in others. The name *Stenella attenuata* (Gray, 1846) has been most commonly applied to the pantropical species in the Indian and Pacific Oceans, following True (1903), although Ogawa (1936) used *Prodelphinus froenatus* for a specimen from Japan and Zhou *et al.* (1980) assigned specimens from China to *S. frontalis* (F. Cuvier, 1829). Based on his (Nishiwaki *et al.* 1965) collection and Ogawa's report, Nishiwaki (1967, 1972) listed both *S. attenuata* and *S. frontalis* from Japan, but illustrations for the two species in his 1967 review were drawn after different photographs of the same specimen (published in the 1965 paper). The names most commonly used for spotted dolphins in the Atlantic in recent years (see references cited above) have been *S. attenuata*, *S. frontalis*, *S. plagiodon* (Cope, 1866) and *S. dubia* (G. Cuvier, 1812). The purposes of this paper are to assign the holotype skulls to the two valid species, redescribe the species and present what is known of their geographical variation.

MATERIALS AND METHODS

Varying combinations of external and skeletal data were available for 210 spotted dolphins from the Atlantic Ocean, 255 from the Indian and Pacific Oceans and 5 from unknown localities. The specimens examined are listed below in the species accounts. Published locality records (in addition to those listed below for specimens) for the Atlantic came from Pernety (1769), F. Cuvier (1829), True (1885, 1889), Lütken (1889), Cuní (1918), Nichols



Figure 1. Development of color patterns in the Atlantic (top three: juvenile, subadult and adult) and pantropical (bottom two: juvenile and adult) spotted dolphins.

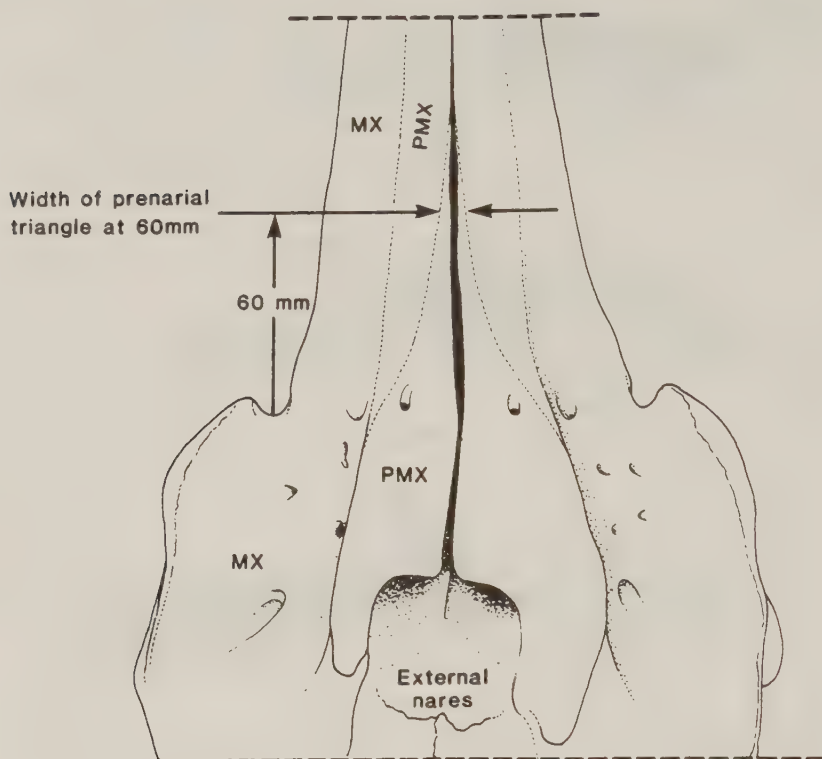


Figure 2. The measurement Width of Prenarial Triangle at 60 mm.

(1920), Allen (1925, 1931), Gunter (1941), Brimley (1946), R. Murphy (1947), Fraser (1950, 1966), Moore (1953), Caldwell (1955, 1960), Kellogg (1955), Cadenat (1956, 1959), Miller and Kellogg (1955), Springer (1957), Cadenat and Lassarat (1959), Mahnken and Gilmore (1959), Schevill and Watkins (1962), Caldwell and Caldwell (1966), Mitchell (1970), van Bree (1971a, 1975), Mörzer Bryns (1971), Caldwell *et al.* (1971), G. Murphy (1979), Schmidly (1972, 1981), Erdman *et al.* (1973), Mercer (1973), Lowery (1974), Brownell and Praderi (1976), Scientific Event Alert Network (1975–1982), Dupuy and Maigret (1976, 1978), Taruski and Winn (1976), Shane (1977), Sutherland and May (1977), Schmidly and Shane (1978), Pinedo and Castello (1980), Fritts and Reynolds (1981), Winn (1982), Fritts *et al.* (1983), Lagendijk (1984), Minasian *et al.* (1984), de Oliveira Gomes (1984), and Best *et al.* (1985). Contributors of unpublished specimen and locality data in addition to the data in the authors' files are listed in the acknowledgments below. All sightings of spotted dolphins were treated as unidentified unless accompanied by description or photographs documenting diagnostic characters. Other records were considered to be of unidentified spotted dolphins (listed below).

External measurements (in cm) follow Norris (1961). Skeletal characters

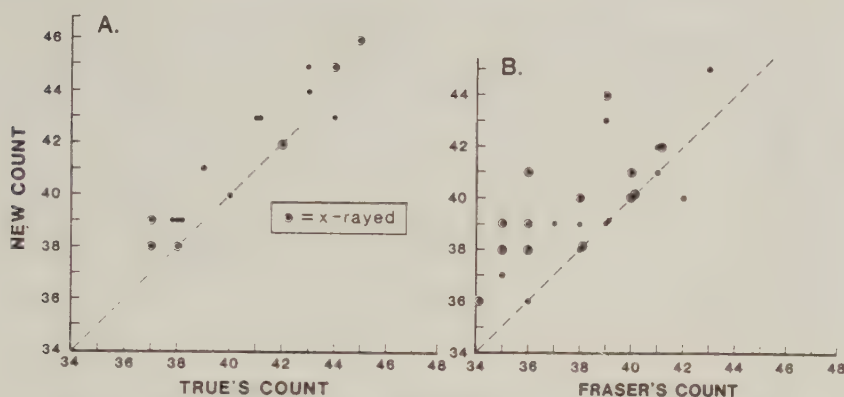


Figure 3. Comparison of highest rostral tooth counts in spotted dolphin skulls made by authors and by True (A) and Fraser (B).

(measured in mm) follow Perrin (1975), with the addition of the character Width of the Prenarial Triangle at 60 mm (Fig. 2). Distal fusion of maxillaries and premaxillaries was used as a criterion for inclusion of skulls in adult series (Perrin 1975). Where this information was not available, sexual maturity was used as a criterion of cranial maturity where possible. Specimens were adjudged physically mature (for inclusion in adult series of postcranial skeletons) if all vertebral epiphyses were fused to the centra.

It is often difficult to count the teeth in a dolphin skull accurately because of dried tissue adhering to the tip of the rostrum or mandible and because the anterior-most teeth are very small and may be lost or buried in the bone. We found that it was frequently necessary to carefully dissect the tips of the rostrum and mandible to expose the anterior-most teeth or alveoli. When this would cause significant damage or when the curator in charge would not allow it, where feasible we made anterior tooth counts from x-rays of the jaw tips. Counts obtained in these ways were often higher than those obtained by earlier workers for the same skulls (Fig. 3). We encountered difficulty in obtaining accurate counts for the mandibular tooththrows because the first one or two teeth were often completely buried in the bone. We therefore used the rostral counts in our analyses. To minimize the biasing effect of loss of the first upper tooth or two in preparation, we used highest rostral tooth count regardless of whether it was the left or right. For some skulls, some rostral teeth were obviously missing at the tip of the rostrum, and the original number could not be estimated with confidence. In these cases, the minimal count was used (*e.g.*, for a tooth count of "more than 38," a value of 39 was used). The expected effect on the analyses would be to decrease the precision of a discriminant function based on the specimens but not inject a bias, as the numbers of such skulls were about the same for the two species.

Similar problems were encountered with vertebral counts. The total number of vertebrae proved to be diagnostic for the two species (*see below*), but many

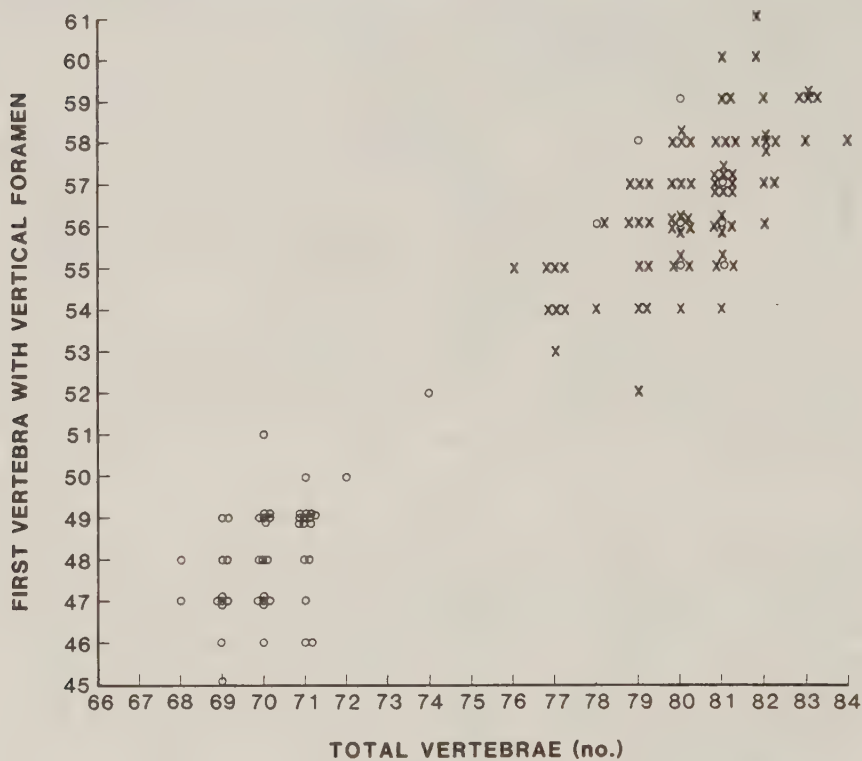


Figure 4. Scatterplot of position of first vertebra with vertically perforating foramen on total number of vertebrae for Atlantic (dots) and Pacific and Indian Ocean (x's) spotted dolphins.

museum specimens lack one or more terminal vertebrae. The terminal caudal series tapers rapidly, and we were sometimes able to estimate confidently the number of missing vertebrae by comparison with an intact specimen. Other specimens had too many vertebrae missing to allow this estimation. We identified these specimens to the two species by referring to the position of the first caudal vertebra bearing a vertically perforating foramen; this character is highly correlated with total number of vertebrae (Fig. 4).

The skull character Width of the Prenarial Triangle at 60 mm was developed only after most of the museum material had been examined. In some cases it was feasible to re-examine the skulls; in others the measurement was made from a photograph taken perpendicular to the long axis of the skull.

The computer programs used in our multivariate analyses were from the BMDP package (Dixon 1985); these were P4M (factor analysis) and P7M (stepwise discriminant analysis). The factor analysis was performed on standardized data (for each character, mean = zero and standard deviation = one). The number of factors was limited to the number of eigenvalues greater than

1.0. The initial unrotated factors (which were the principal components) were rotated orthogonally, optimizing the distribution of the variance between the two factors (patterning). The convergence criterion for rotation was 0.00001. Kaiser's normalization was employed. In the stepwise discriminant analysis, the F-to-enter at step 0 for a variable was computed from a one-way analysis of variance on the variable for the groups used in the analysis. A variable was removed from the analysis if its F-to-remove was less than the initial F-to-enter. Maximum forced level was set at 1 for all variables.

Specimens examined but not identified as to species—Massachusetts: 1 (USNM 7071—mandible). Florida: 2 (USNM 218344—damaged juvenile cranium, USNM 23414—partial postcranial skeleton). St. Helena: 1 (GM 969—scrimshawed ramus).

Previously unpublished sighting records for unidentified spotted dolphins in the Atlantic (in addition to those from specimens listed above; sources, when other than authors, listed in ACKNOWLEDGMENTS): western North Atlantic, 1 (42°58'N latitude, 59°11'W longitude—EDM); Azores, 1 (37°46'N, 24°44'W—EDM); off New York, 5 (41°00'N, 71°43'W; 40°50'N, 71°47'W; 40°53'N, 71°29'W; 40°54'N, 71°27'W; 40°58'N, 71°38'W); North Carolina and offshore, 3 (Rodanthe; 36°00'N, 74°39'W; 35°17'N, 74°15'W); Florida and offshore, 2 (Destin; 30°48'N, 78°28'W—EDM); Caribbean, 8 (near St. Croix; 20°21'N, 84°40'W; 19°42'N, 84°10'W; 18°22'N, 83°09'W; 17°38'N, 63°35'W—EDM; 14°38'N, 70°53'W; 14°22'N, 71°16'W; Santa Margarita Island); off Panama, 1 (9°51'N, 79°22'W); near Canary Islands, 1 (28°05'N, 63°35'W).

RESULTS OF THE DISCRIMINANT ANALYSIS

The two apparent species differ in the total number of vertebrae as well as in color pattern (*see* redescrptions below). Where vertebral count is available, all specimens with the Atlantic endemic color pattern have about 70 vertebrae and all those with the pantropical pattern have about 80. There is no overlap (Table 1, Fig. 5). Based on this finding, we assigned all specimens with no coloration data but with 74 or more vertebrae to the pantropical species and all those with 72 or fewer to the Atlantic endemic species. This yielded a comparative base of 60 Atlantic specimens of the former and 87 of the later.

Skulls of the two species overlap in every character (*see* below in species redescrptions). We were able to separate the two series, however, by considering several characters simultaneously. Four characters were sufficient to provide separation: Width of Rostrum at $\frac{1}{2}$ Length, Width of Rostrum at $\frac{3}{4}$ Length, Width of Prenarial Triangle at 60 mm, and Highest Rostral Tooth Count. Because of the considerable geographic variation in size in both species (*described* below), we standardized the three width measurements through division by Postorbital Width.

The endemic species tends to have a proportionately wider rostrum tip, a shorter prenarial triangle (narrower at 60 mm) and fewer teeth. Discriminant analysis using the four characters correctly identified all of the specimens (Table

Table 1. Specimens of spotted dolphins from Atlantic for which both color pattern and vertebral count are known. Values in parentheses are estimates for specimens with one or more terminal vertebrae missing.

Locality	Specimen number	Color pattern	Vertebrae	Reference
Mid-North Atlantic				
1. Azores	EDM 760	Endemic	68	Mitchell 1970
2. Azores	AMNH 239111	Endemic	69	Mitchell 1970
3. Near Azores	UZMC <i>Prodelphinus</i> no. 4	Endemic	(71)	Lütken 1889
4. 46°20'N, 38°44'W	EDM 786	Endemic	70	—
5. 38°40'N, 49°W	UZMC <i>Prodelphinus</i> no. 11	Endemic	70	Lütken 1889
Western North Atlantic				
6. Massachusetts	USNM 550016	Pantropical	81	—
7. New York	USNM 550353	Endemic	71	—
8. Off New Jersey	MCZ 51074	Endemic	(70)	—
9. Off New Jersey	MCZ 51294	Endemic	(71)	—
10. Virginia	USNM 504758	Endemic	71	—
11. Off North Carolina	AMNH 239117	Endemic	70	—
12. Off North Carolina	EDM 694	Endemic	69	—
13. Off North Carolina	EDM 695	Endemic	(71)	—
14. Off North Carolina	USNM 22017	Endemic	(69)	True 1889
15. North Carolina	USNM 504321	Endemic	71	—
16. North Carolina	USNM 504322	Endemic	70	—
17. North Carolina	USNM 504736	Endemic	70	—
18. North Carolina	USNM 504748	Endemic	70	—
19. North Carolina	USNM 504762	Endemic	(70)	—
20. North Carolina	USNM 504876	Endemic	70	—
21. North Carolina	USNM 504901	Endemic	68	—
22. North Carolina	USNM 550024	Endemic	69	—
23. North Carolina	USNM 550025	Endemic	69	—
24. North Carolina	USNM 550098	Endemic	71	—
25. North Carolina	USNM 550102	Endemic	71	—
26. Off South Carolina	EDM 696	Endemic	(71)	—
27. Off South Carolina	EDM 697	Endemic	(71)	—
28. South Carolina	USNM 500858	Endemic	69	—

Table 1. Continued.

Locality	Specimen number	Color pattern	Vertebrae	Reference
29. Off Georgia	EDM 844	Endemic	70	—
30. Off Georgia	USNM 261364	Endemic	69	—
31. Off Georgia	Fetus of 261364	Endemic	71	—
32. Off Florida	EDM 700	Endemic	(71)	—
33. Off Florida	EDM 701	Endemic	(71)	—
34. Florida	UF R-1-SF	Pantropical	(77-81)	—
35. Florida	UF R-2-SF	Pantropical	80	—
36. Florida	UF R-4-SF	Pantropical	(80)	—
Gulf of Mexico				
37. Florida	UF R-G-2-SF/SP	Endemic	67	—
38. Florida	USNM 21915	Endemic	70	True 1885
39. Texas	USNM 292070	Endemic	69	Caldwell and Caldwell 1966
Caribbean				
40. Off Haiti	UZMC <i>Prodelphinus</i> no. 14	Endemic	70	Lütken 1889
41. Off Puerto Rico	EDM 808	Endemic	69	—
42. Off Puerto Rico	AMNH 239116	Endemic	69	—
43. Lesser Antilles	EDM 803	Endemic	70	—
44. Off Venezuela	AMNH 239113	Endemic	71	—
45. Off Venezuela	EDM 706	Endemic	71	—
46. Off Venezuela	EDM 710	Endemic	(70)	—
47. Off Venezuela	AMNH 239114	Endemic	70	—
48. Off Venezuela	AMNH 239112	Endemic	72	—
Mid-Tropical Atlantic				
49. 6°46'N, 24°35'W	AMNH 39092	Pantropical	(80)	Murphy 1947
50. 2°44'N, 29°W	UZMC <i>Prodelphinus</i> no. 8	Pantropical	79	Lütken 1889
Africa				
51. Ivory Coast	ZMA 13.546	Endemic	(70)	van Bree 1971
52. Ivory Coast	ZMA 22.964	Endemic	(~66)	Cadenat and Lassarat 1959
53. Gulf of Guinea	BMNH Atlantic	Pantropical	81	Fraser 1950

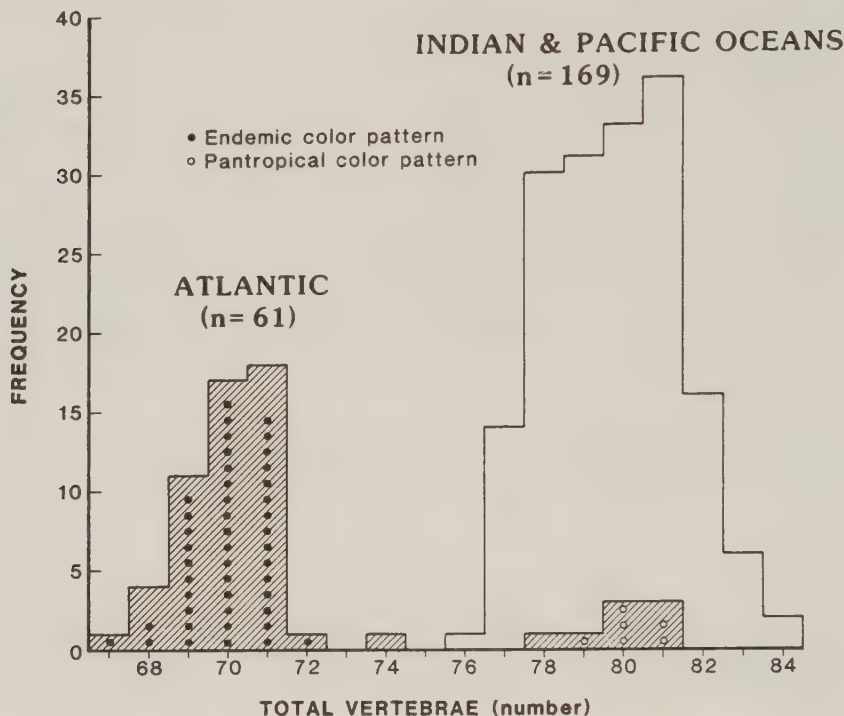


Figure 5. Number of vertebrae in spotted dolphins. Atlantic specimens (hatched) superimposed on Indian and Pacific Ocean specimens. Dot = Atlantic endemic color pattern; open circle = pantropical pattern (all Indopacific specimens had pantropical pattern). Indopacific data from Nishiwaki *et al.* (1965), Ross (1984) and Lütken (1889) and from specimens included in Perrin (1975) and Perrin *et al.* (1979).

2, Fig. 6), including juvenile specimens (CB length 305–414 mm). The holotype specimens are each clearly associated with one of the two species with high probability ($P < 0.01$). The holotypes of *Steno attenuatus* Gray, 1846; *S. capensis* Gray, 1865 and *Delphinus brevimanus* Wagner, 1846 belong to the pantropical species, and those of *Delphinus doris* Gray, 1846; *D. froenatus* F. Cuvier, 1829; *D. frontalis* G. Cuvier, 1829 and *D. plagiodon* Cope, 1866 belong to the endemic species.

All specimens of spotted dolphins from the Indian and Pacific Oceans for which color pattern and/or vertebral count are known are of the pantropical species. Application of the discriminant function based on the Atlantic material to a series of Indopacific skulls resulted in correct classification of all but two of the 115 specimens (lower panel in Fig. 6). The Indopacific specimen with a value of 0.3 for the canonical variable is an aberrant skull. The rostrum is extremely blunt and broad (36 mm at $\frac{3}{4}$ length; Perrin 1975, fig. 41) and has a highest rostral tooth count of only 38, the lowest value for the specimens of the pantropical species included in the analysis. The dolphin was captured

Table 2. Statistics for stepwise discriminant analysis of skulls of *Stenella frontalis* and *S. attenuata*.

Character	F-value to enter	Order of entry	Coefficients ^a	Classification functions ^b	
				<i>S. frontalis</i>	<i>S. attenuata</i>
W.d. of rostr. at $\frac{3}{4}$ ln/po w.d.	167.38	1	0.0153	0.0317	-0.0984
W.d. of prenar. triangle at 60 mm/po w.d.	58.94	2	-0.0379	-0.3063	0.0158
Highest rostral tooth count	23.03	3	-0.1621	12.7033	14.0818
W.d. of rostr. at $\frac{1}{2}$ ln/po w.d.	6.85	4	0.0203	1.8991	1.7263
Constant			-2.3379	-500.8247	-494.2775

^a For discriminant function; standardized by pooled within-group variances.^b Used with original proportional measurements and tooth count. Add products of measurement ($\div$ po width) or tooth count and corresponding function values to constant; classify as *S. frontalis* or *S. attenuata* depending on which results in highest value for classification function.

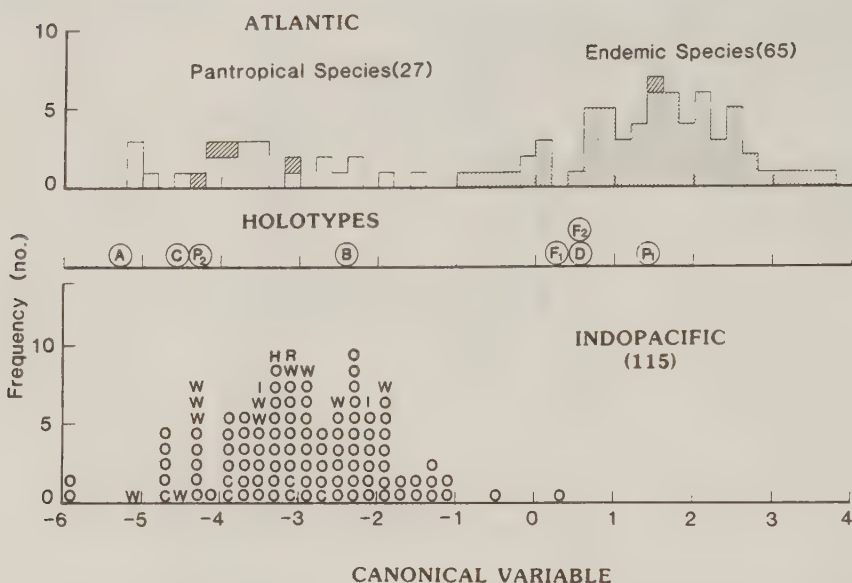


Figure 6. Frequency distributions of specimens of spotted dolphins on first canonical variable. Atlantic specimens (top panel) identified to the endemic and pantropical species based on color pattern and/or number of vertebrae. Juvenile specimens hatched. Holotype specimens (middle panel): A = *Steno attenuatus* (juvenile), B = *Delphinus brevimanus*, C = *S. capensis*, D = *P. Doris*, F1 = *D. froenatus*, F2 = *D. frontalis*, P1 = *D. plagiodon*, P2 = possible holotype of *D. pseudodelphis*. Indopacific specimens (bottom panel) include coastal (C) and oceanic (O) specimens from the eastern Pacific and skulls from Hawaii (H), the western Pacific (W), the Indian Ocean (I) and the Red Sea (R).

with other pantropical spotted dolphins and had the typical pantropical color pattern and 81 vertebrae. The other Indopacific specimen with an anomalously high value for the canonical variable (-0.5) was also an eastern Pacific specimen with a relatively broad rostrum (32 mm at $\frac{3}{4}$ length) and tooth count at the low end of the range for the species (38). This result indicates that the discriminant function cannot be used to identify skulls with certainty, but it does not affect the conclusions concerning the holotype specimens; the holotypes having values similar to those of the aberrant eastern Pacific specimens are from the Atlantic and are clearly associated with the distribution of Atlantic specimens known to be of the endemic species.

For purposes of the species redescrptions below, an additional 35 Atlantic specimens lacking data on coloration or number of vertebrae were assigned to the two species using the discriminant function; these had data for all four of the skull characters. Another 12 specimens with missing values for one or more of the four characters were identified by comparing the values for the remaining characters with those for the two Atlantic series. If a skull was outside the range for one of the species in any of the characters but within it for the other for all characters, it was assigned to the latter.

REVIEW OF THE NOMINAL SPECIES

Many names have been applied to spotted dolphins. Here we review the names and re-assign them to one or the other of the two valid species where possible. We have drawn heavily on the comprehensive work by Hershkovitz (1966). Additional discussion of many of the nominal species was given by Perrin (1975).

D[elphinus] dubius G. Cuvier, 1812

Cuvier did not designate a holotype specimen for this species, but he later (1823) published measurements of a skull under *D. dubius*. A skull of uncertain origin in the Paris Museum (A-3033, labeled *D. froenatus*) conforms precisely to these measurements. Examination of the 19th century material of unknown origin in the Paris Museum, however, indicates that G. Cuvier's (1812) "several skulls" possibly included specimens of both spotted species; it therefore would not be prudent to designate A-3033 as a lectotype for *D. dubius*; the name best remains a *nomen nudum*. Other combinations include *Prodelphinus dubius* (H. Gervais in P. J. van Beneden and P. Gervais, 1880), *Clymenia dubia* (Flower, 1884) and *Stenella dubia* (Hershkovitz, 1966).

Delphinus pernettensis de Blainville, 1817

This species was based on a sketch published by Pernety (1769) of a dolphin captured in the Cape Verde Islands off West Africa. The specimen was not saved. Although the strongly defined cape shown in the sketch is evocative of the color pattern of the pantropical spotted dolphin, the identification cannot be certain. The point is moot, as the name has been suppressed by the International Commission of Zoological Nomenclature (Opinion 1067) following van Bree (1971b). Other combinations and emended forms: *D. Pernettyi* (Desmarest, 1822), *Delphinorhynchus Pernettyi* (Lesson, 1827), *Delphinus Pernetyi* (True, 1885), *D. pernettensis* (Philippi, 1893) and *Stenella pernettyi* (Hershkovitz, 1966).

Delphinus malayanus Lesson, 1826

Lesson (in Lesson and Garnot 1826) based this species on a specimen harpooned between Java and Kalimantan (Borneo). There is no holotype specimen. We believe that the dolphin in the crude sketch included in the description (prepared by an artist based on Lesson's field observations) cannot be identified with any confidence. It could be a specimen of the pantropical spotted dolphin, but it could equally well represent a specimen of *Stenella longirostris*, *Steno bredanensis*, *Sousa chinensis*, or even a sun-darkened specimen of *Stenella coeruleoalba* or *Delphinus delphis*. Weber (1923) following Schlegel (1841) applied *Prodelphinus malayanus* to spotted dolphins from Indonesia. In our opinion, *D. malayanus* should be considered a *nomen nudum*. Other combinations: *Steno Malayanus* (Gray, 1846), *Prodelphinus malayanus* (True, 1889).

D[elphinus] velox G. Cuvier, 1829

G. Cuvier based *D. velox* on a specimen captured by Dussumier between Ceylon and the Equator. The holotype specimen is a mounted skin in the Paris Museum (No. 17 of the Catalogue de la Galerie de Zoologie). Pucheran (1856) reported measurements of the mounted skin. He also noted that, while F. Cuvier (1836) had reversed himself and stated that the animal was uniformly dark-gray below rather than spotted, he (Pucheran) could still see traces of dark ventral spots on the stuffed skin. As noted by Perrin (1975), the shape, coloration (mottled below) and tooth counts as described by F. Cuvier (1829) from notes by Dussumier, who collected the specimen, indicate that it was a pantropical spotted dolphin. Trouessart (1898) placed the species tentatively in the synonymy of *Delphinus malayanus* Lesson but dropped it from the subsequent edition of his list (1904–1905). Other than in the reiteration of Trouessart's (1898) synonymy by Ellerman and Morrison-Scott (1951), the name has not been applied to spotted dolphins in this century and therefore should be considered a *nomen oblitum*.

Delphinus frontalis G. Cuvier, 1829*Delphinus froenatus* F. Cuvier, 1829

The respective holotype specimens of these two species were both harpooned by Dussumier off Cape Verde, West Africa. Perrin (1975) suggested that they were pantropical spotted dolphins, based on position of the flipper stripe (running below the eye to the gape, rather than to the eye as in western Atlantic specimens of the endemic spotted dolphin), but it is now apparent that the endemic species varies in this character (see discussion of geographical variation below). The holotype specimens of *D. frontalis* and *D. froenatus* have recently been identified in the Paris Museum (MNHN A-3035 and A-3034, respectively, D. Robineau, pers. comm.), and they conform with the endemic species (F1 and F2 in Fig. 6). The species is known to occur in the area from other evidence (Lütken 1889, specimen no. 2, with 68 vertebrae and upper tooth count of 37). Both names have been used extensively in the literature (Hershkovitz 1966, Honacki *et al.* 1982). *D. frontalis* was published first (Fraser 1950). Other combinations and emendations: *Prodelphinus frontalis* (H. Gervais in P. J. van Beneden and P. Gervais, 1880), *Clymenia frontalis* (Flower, 1884), *Stenella frontalis* (Fraser, 1950), *Delphinus fraenatus* (F. Cuvier, 1836), *D. frenatus* (Gray, 1846), *Tursio fraenatus* (Gray, 1866), *Prodelphinus fraenatus* (Gervais in van Beneden and Gervais, 1880), *Clymenia fraenata* (Flower, 1884), *Prodelphinus froenatus* (True, 1889) and *P. fraenatus* (Beddard, 1900).

Delphinus pseudodelphis Wiegmann, 1840 or earlier

A plate (no. 38) in von Schreber (1840, as cited by Wagner 1846) consists of three views of a skull with this name as the legend. There is no information on the species in the text. Wagner in the 1846 edition of *Schreber's Saeugthiere* noted that a skull in the Leiden collection (Zool. Mus. Berlin no. 12009, from

an unknown locality) thought by Schlegel (1841) to be the holotype was probably a different skull. We have examined photographs of it and agree; either the figures are extremely inaccurate, or a different skull is involved. The maxillary foramina and the nasal bones in particular are of different configurations in the two specimens. The highest rostral and mandibular tooth counts in the Leiden skull are only 41 and 39, respectively, as opposed to 44 and 46 in Wiegmann's figure. The skull figured by Wiegmann, however, (like the ZMB specimen—P2 in Fig. 6) does conform well with the skull of the pantropical species. The rostrum is narrow distally, the prenasal triangle long, and tooth counts very high, above the range for the endemic species. We therefore believe the name *D. pseudodelphis* to be a valid synonym for the pantropical species. It has been used in a substantive manner only once in this century, by Oliver (1922), as *Stenella pseudodelphis*, and we therefore propose that it be considered a *nomen oblitum*. *Prodelphinus pseudo-delphis* (True, 1889) was a later combination.

Delphinus loriger Wiegmann, 1841(?)

Hershkovitz (1966), followed by Hall (1981), included this species in the synonymy of *Stenella dubia*, but the figure of external appearance that comprises the description is clearly of a common dolphin, *Delphinus delphis* Linnaeus.

Delphinus Rappii Reichenbach, 1846

The holotype specimen of this species (from the Cape of Good Hope and in the Stuttgart Museum) has 20–30 teeth in the lower jaw and 22 in the upper. It was described earlier by Rapp (1837) under "*Delphinus capensis* Gray" but is not of the same species as the holotype of *D. capensis* Gray, 1828, which was a specimen of *D. delphis* (Hershkovitz 1966); the tooth counts as given by Rapp are too low. We have not examined the specimen but believe that Hershkovitz (1966) was not justified in including the name in the synonymy of *Stenella dubia*. Rapp noted a similarity to *Delphinus malayanus* Lesson (discussed above), but this was likely based on external appearance. The crude illustration appended to his description indeed resembles the (equally crude) illustration in Lesson's description, but neither much resembles a spotted dolphin. Until the holotype skull can be critically examined, the species should remain *incertae sedis*. In any case, the name has not been used since 1846 and should be considered a *nomen oblitum*.

Steno attenuatus Gray, 1846

This nominal species was based on a juvenile skull from an unknown locality (BMNH 347.b.). The skull is clearly a specimen of the pantropical species (Fig. 6), possibly from India (Gray 1843). The name has been in continuous use for spotted dolphins in the Indian and Pacific Oceans since True (1894) applied it to several specimens from the Indian Ocean. The name *Delphinus*

attenuatus Gray, 1843 appeared earlier but without description or figure and therefore is a *nomen nudum*. Later combinations: *Clymenia attenuatus* (Flower, 1884), *Clymenia attenuata* (Hector, 1885), *Prodelphinus attenuatus* (Flower, 1885), *Stenella attenuata* (Iredale and Troughton, 1934).

Delphinus brevimanus Wagner, 1846

Delphinus? microbrachium Gray, 1850

These two species were based on the same specimen of the pantropical spotted dolphin collected near Singapore and figured (external appearance only) by Hombron and Jacquinot (1842–1853) under the name "*dauphin à petites pectorales*." The skull of the holotype specimen (MNHN 1882-113; B in Fig. 6) was described by Jacquinot and Pucheran in Hombron and Jacquinot (1853). Neither name has been used in this century, and therefore we consider each to be a *nomen oblitum*. Other combinations: *Steno brevimanus* (Gray, 1866), *Prodelphinus brevimanus* (H. Gervais in P. J. van Beneden and P. Gervais, 1880).

Delphinus Doris Gray, 1846

The holotype specimen of this species is a skull (BMNH 352.a.) from an unknown locality that conforms well with the endemic Atlantic species (D in center panel of Fig. 6). Other combinations: *Tursio Doris* (Gray, 1866), *Clymene doris* (Gray, 1866), *Clymenia Doris* (Gray, 1868) and *Prodelphinus doris* (True, 1885 and Flower, 1885).

Delphinus albirostratus Peale, 1848

The holotype specimen of this species was collected in the Phoenix Islands in the Pacific but subsequently lost. As noted by Perrin (1975), the figure in Peale is of a pantropical spotted dolphin. For a time the species was placed in *Lagenorhynchus* (Dall 1874, True 1889). The figure for *D. albirostratus* in Cassin (1858) is in plate 6 (fig. 2), not Plate 7 as stated in Cassin's text.

Delphinus mediterraneus Loche, 1860

Hershkovitz (1966) placed this species in synonymy with *Stenella frontalis* (G. Cuvier), but Loche's description of the color pattern identifies the type specimen as a striped dolphin, *Stenella coeruleoalba* (Meyen, 1833), a fact recognized by Hall (1981). *D. delphis mediterranea* (Nobre, 1900) is a later combination.

Delphinus asthenops Cope, 1865

Delphinus crotaphiscus Cope, 1865

Honacki *et al.* (1982), following Hall (1981), stated that [*Stenella*] *dubia* includes these two nominal species. Cope (1865), however, believed that they

belonged "to the same group as the styx [and] euphrosyne" (now in the synonymy of the striped dolphin, *Stenella coeruleoalba*). We have examined the two syntype skulls of *D. asthenops* (PANS 2595 and 2956 in the Museum of the Peabody Academy) and agree with Cope. The holotype specimen of *D. crotaphiscus*, formerly at the MCZ, has been lost. In any case, it is clear from Cope's description that the skull was not of a spotted dolphin. (Skull characters separating spotted dolphins from other species in *Stenella* are summarized in Perrin *et al.* 1981). Other combinations and emended forms: *Clymenia esthenops* (Gray, 1871), *Clymenia aesthenops* (Dall in Scammon, 1874), *Stenella asthenops* (Hershkovitz, 1966), *Clymenia crotaphiscus* (Gray, 1871), *Prodelphinus crotaphiscus* (Trouessart, 1898), *Stenella crotaphiscus* (Hershkovitz, 1966) and [*Stenella*] *crotaphiscus* (Honacki *et al.*, 1982).

Delphinus clymene Gray, 1850

True (1889) placed this species (and its later forms *Delphinus normalis* Gray, 1866 and *Clymenia normalis* Gray, 1868) in synonymy with *Prodelphinus frontatus* (F. Cuvier); this was followed by Hall (1981) in his synonymy of *Stenella frontalis*. Later workers, however, recognized the species as distinct and valid, as *Stenella clymene* (Hershkovitz 1966, Perrin *et al.* 1981).

Steno capensis Gray, 1865

The holotype skull (BMNH 1519.a.), from the Cape of Good Hope, represents the pantropical species (C in center panel of Fig. 6). Other combinations: *Clymenia Capensis* (Flower, 1884) and *Prodelphinus capensis* (Trouessart, 1898).

Clymene punctata Gray, 1866

The holotype skull of this species, from Cape Verde, West Africa, was destroyed in Berlin during World War II (Fraser 1950), but upper tooth counts (42) obtained by True (1889)—which are likely to be low (see MATERIALS AND METHODS)—and the color pattern as depicted by Gray (1866) identify this specimen as a pantropical spotted dolphin. Gray's illustration shows an animal with a well-defined cape, no spinal blaze, a "chevron" blaze between dorsal fin and flukes, and division of the peduncle into dark upper and light lower halves; all of these are features of the pantropical species' pattern. *Delphinus punctatus* (Gray, 1866) is a later combination.

Delphinus plagiodon Cope, 1866

This species was based on a skull (USNM 3884) from an unknown locality. The discriminant analysis identifies it as a specimen of the endemic species (P1 in Fig. 6). It very closely resembles large skulls of the species from the U.S. Atlantic Coast (discussed below) and may have been collected there. Other

combinations: *Prodelphinus plagiodon* (True, 1885), *Stenella plagiodon* (Kellogg, 1940).

Steno consimilis Malm, 1871

Hershkovitz (1966) placed this species in the synonymy of the spinner dolphin, *Stenella longirostris* (Gray, 1828). We did not examine the holotype skull (in the Technological Institute, Norrköping, Sweden), which is from Madagascar, but as illustrated by Malm it is a typical skull of the pantropical spotted dolphin, with 45 rostral teeth and 40 mandibular on each side.

Prodelphinus graffmani Lönnberg, 1934

The type specimen (in the State Museum of Natural History, Stockholm) consists of the mounted skin and damaged skull of a large spotted dolphin harpooned near Acapulco, Mexico, in the eastern tropical Pacific. Perrin (1975) found all spotted dolphins in the eastern Pacific to be conspecific and placed *P. graffmani* in the synonymy of *Stenella attenuata* as a subspecies, *S. a. graffmani*. *Stenella graffmani* (Kellogg, 1940) is a later combination.

Name Priority

For the pantropical spotted dolphin, the valid synonyms *Delphinus velox* G. Cuvier, 1829, *D. pseudodelphis* Wiegmann, 1840 (or earlier) and possibly *D. brevimanus* Wagner, 1846 antedate *Steno attenuatus* Gray, 1846. However, because of the long and continuous use of the latter and its emended forms and binomial recombinations, as well as because none of the first three names has had currency in this century, we are proposing that *Stenella attenuata* be used for this species, as a *nomen conservandum* (under Article 23b of the International Code of Zoological Nomenclature).

The senior synonym for the Atlantic spotted dolphin is *Delphinus frontalis* G. Cuvier, 1829. The name in various forms has also been in continuous use since its appearance, and we propose that *Stenella frontalis* be used for this species.

REDESCRIPTION OF *STENELLA FRONTALIS*

- 1829. *D[elphinus] frontalis* G. Cuvier, Règne Animal, 1, p. 288.
- 1880. *Prodelphinus frontalis*. Gervais, in van Beneden and Gervais, Ostéographie des Cétacés, p. 605, pl. 38, fig. 3.
- 1884. [*Clymenia*] *frontalis*. Flower, Proc. Zool. Soc. London, 1883, p. 512.
- 1950. *Stenella frontalis*. Fraser (in part), Atlantide Rep., 1, p. 61.
- 1829. [*Delphinus*] *froenatus* F. Cuvier, in Geoffroy Saint-Hilaire and F. Cuvier, Histoire Naturelle des Mammifères, 3, Sect. 58 (unpaginated).
- 1836. *Delphinus fraenatus*. F. Cuvier, Histoire Naturelle des Cétacés, p. 155, pl. 10, fig. 10.

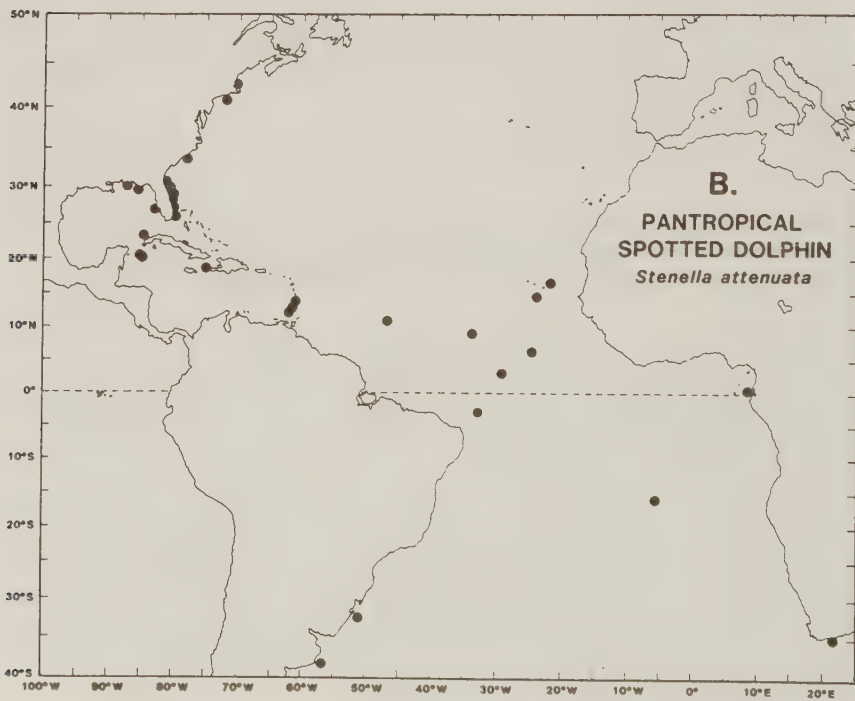
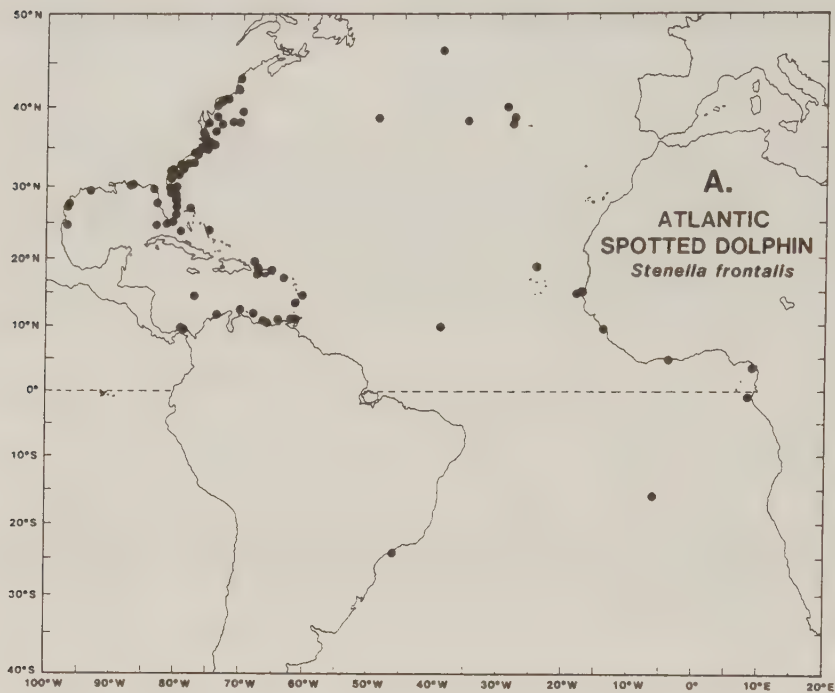
1846. *Delphinus frenatus*. Gray, Zoology of the voyage of *H.M.S. Erebus and Terror*, 1, p. 39.
1866. *Tursio fraenatus*. Gray, Catalogue of seals and whales in the British Museum, p. 256.
1880. *Prodelphinus fraenatus*. H. Gervais, in van Beneden and Gervais, *Ostéographie des Cétacés*, p. 605, pl. 38, fig. 4.
1884. [*Clymenia*] *fraenata*. Flower, Proc. Zool. Soc. London, 1883, p. 512.
1889. *Prodelphinus froenatus*. True, Bull. U.S. Nat. Mus., 36, p. 68, 70, 73, 166, pl. 19, fig. 1 & 2, pl. 20, fig. 1.
1900. *Prodelphinus fraenatus*. Beddard, Book of whales, p. 261.
1846. *Delphinus Doris* Gray, Zoology of the voyage of *H.M.S. Erebus and Terror*, 39, pl. 20.
1866. *Tursio Doris*. Gray, Catalogue of seals and whales in the British Museum, p. 255.
1866. *Clymene doris*. Gray, Proc. Zool. Soc. London, 1866, p. 214.
1868. *Clymenia doris*. Gray, Synopsis of the whales and dolphins in the British Museum, p. 6, pl. 20.
1885. *Prodelphinus doris*. True, Rep. U.S. Nat. Mus., 1884, p. 317, pl. 1–6.
1885. *Prodelphinus doris*. Flower, List of specimens of Cetacea in the Zoological Department of the British Museum, p. 26.
1866. *Delphinus plagiodon* Cope, Proc. Acad. Nat. Sci. Philadelphia, 18, p. 296.
1885. *Prodelphinus plagiodon*. True, Rep. U.S. Nat. Mus., 1884, p. 323, pl. 4, 6.
1940. *Stenella plagiodon*. Kellogg, Nat. Geogr. Mag., 77, p. 83, pl. 19.
1889. *Prodelphinus obscurus* Lütken (not Gray), Vid. Selsk. Skrift., Copenhagen, Nat. Mat. 5(1), p. 43.
1981. *Stenella pernettensis plagiodon* (Cope) of Hall, Mammals of N.A., p. 883.

Holotype and type locality—Adult skull, Muséum National d'Histoire Naturelle, Paris (MNHN) no. A-3035, and mounted skin (no. 25 of the Catalogue de la Galerie de Zoologie) off Cape Verde, West Africa (approximately 15°N, 18°W).

Distribution—Tropical, subtropical and warm temperate Atlantic (Fig. 7a). Not known to occur in Indian or Pacific Oceans. Perrin *et al.* (1978) noted the possible existence of endemic tropical dolphins in the Atlantic and speculated that they may represent forms that arose during Pleistocene isolation of the tropical Atlantic from the Indopacific.

G. Cuvier (1829) stated that *D. dubius* (probably = *S. frontalis*) occurs in European waters. There is a skull of *S. frontalis* in the British Museum (BMNH 1948.5.1.1, acquired from the Rothschild collection and accessioned in 1948) labeled "coast of Europe," but we could find no other record of the species from the eastern Atlantic north of the Cape Verde Islands. Unidentified spotted dolphins reported from the Canary Islands may be of this species (Fig. 7c).

There are two skulls of *S. frontalis* labeled as from St. Helena (UZMC



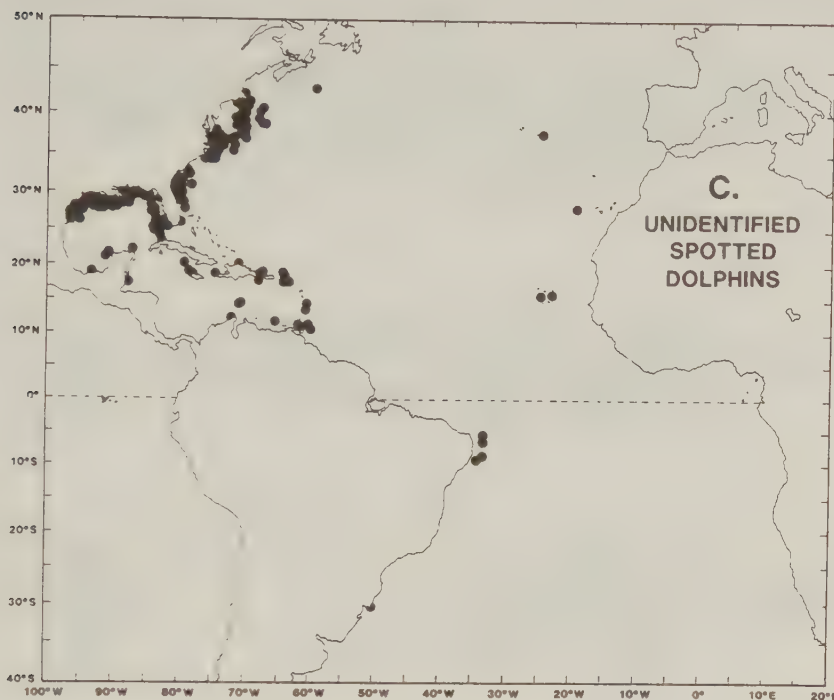


Figure 7. Locality records in the Atlantic for A) *Stenella frontalis*, B) *S. attenuata* and C) unidentified spotted dolphins. Note: the latitude for "Prodelphinus no. 2" in Lütken (1889) should be 19°03'N, not 13°03'N (based on original field data sheets in UZMC).

Prodelphinus no. 1 in the Copenhagen Museum and MNHN A-3031 in the Paris Museum), both collected in the 19th century. All records of spotted dolphins from St. Helena in this century are of the pantropical species, and the fishermen presently living on the island have no knowledge of a second type of spotted dolphin (Perrin 1985a, Perrin and Perrin 1985). As was probably the case for a record of the southern right whale dolphin, *Lissodelphis peronii*, a coldwater species (Perrin 1985a), it is possible that the two early specimens were collected by ships on the way to or from St. Helena. It was common practice aboard whalers and some other vessels to harpoon dolphins for use as food for the crew. It is, of course, also possible that the species formerly occurred at the island or that it visits the island's waters only rarely. The two skulls closely resemble specimens from West African and mid-tropical Atlantic waters (discussed below).

Diagnosis—The color pattern consists of an underlying ground pattern present at birth and superimposed dark ventral and light dorsal spots that develop with maturation (Fig. 1). In the ground pattern, the ventral margin of the dark gray cape (terminology of Perrin 1972) is obscured anteriorly by a spinal blaze (terminology of Mitchell 1970) that sweeps up and back, its apex below the

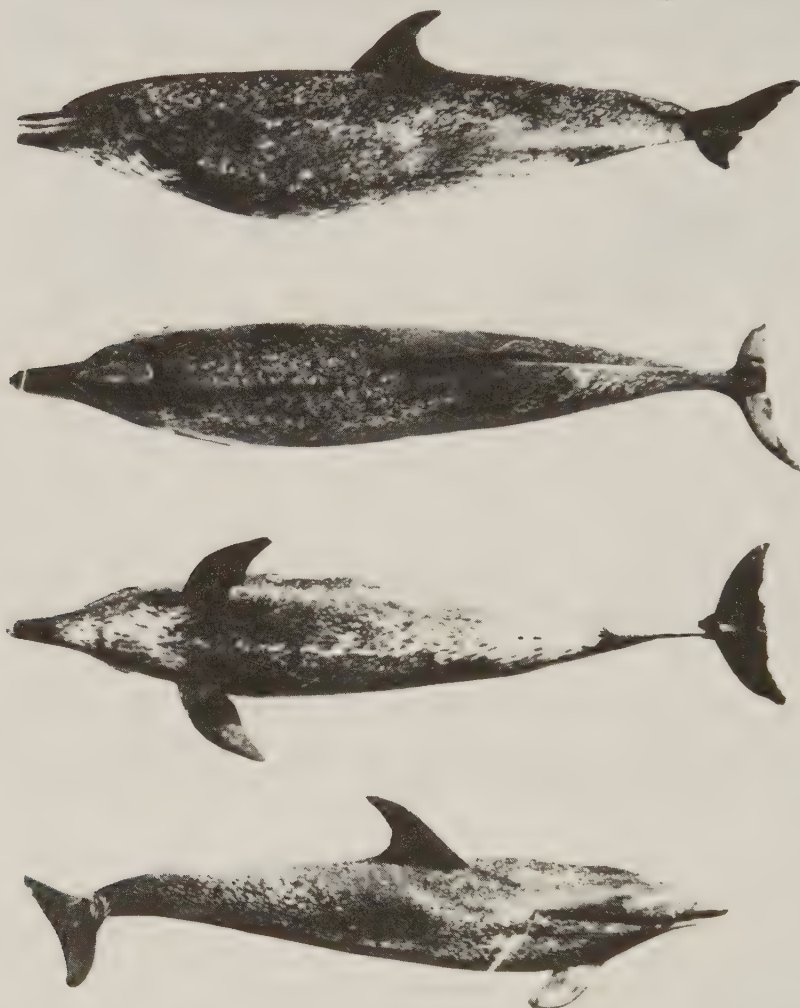


Figure 8. Heavily spotted specimens of *Stenella frontalis*: (top 3) a 206-cm physically mature male (EDM 695) from off the coast of North Carolina and (bottom) a 224-cm male (USNM 253598) from off South Carolina (note spinal blaze).

dorsal fin. The blaze varies individually in length, width and intensity of expression. The combination of spinal blaze and dorsal spotting is unique to this species. The spinal blaze may be nearly obscured by light dorsal spots in mature individuals in some geographical areas, but it is usually at least faintly visible in dorsal view (Fig. 8). The ventral margin of the light gray lateral field begins behind the eye and ends indistinctly in the anal region; it too may be obscured in mature adults in some regions by dark ventrolateral spotting (Fig. 8). The basic delphinid "bridle" of dark-gray-to-black blowhole stripe and eye patch

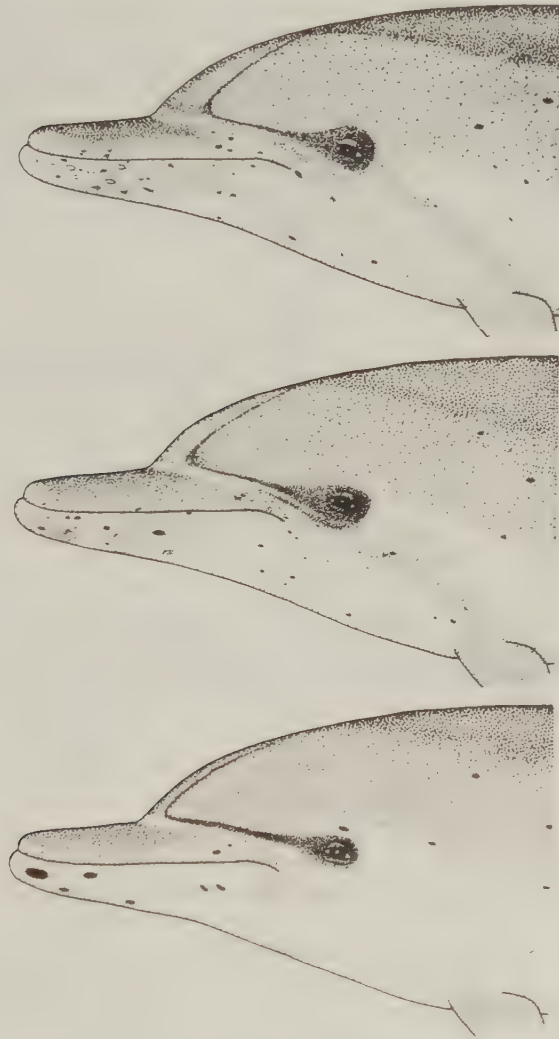


Figure 9. Variation in position of anterior end of flipper stripe in *Stenella frontalis*: (top) behind eye, (middle) lower edge of eye, (bottom) angle of gape. Drawn from photos of (top to bottom) a 205-cm subadult male (EDM 697) from off South Carolina, a 197-cm cranially adult female (EDM 696) from off South Carolina, and a cranially adult 166-cm male (AMNH 239111) from the Azores.

and stripe is present. The blowhole and eye stripes may consist of two or more parallel darker and lighter sub-elements. In young calves there is an irregularly defined extension of the white ventral field up into the lateral field starting at about the level of the anterior insertion of the dorsal fin, giving the animal a blotched appearance. A sharply defined dark gray mark borders the gape pos-

teriorly. The dorsal margin of this mark intersects the ventral margin of the eye stripe several centimeters anterior to the angle of the gape. The flipper stripe consists of two parts: a narrow (less than 5 mm) light line dorsally bordering a wider (about 25–50 mm) darker band with indistinct ventral margin. The flipper stripe may end anteriorly at the eye, between the eye and the gape, or at the angle of the gape; this feature varies both individually and geographically (Fig. 9). When the flipper stripe abuts anteriorly on the gape mark, the junction is delineated with a faint light line. This region of complex interaction of flipper stripe, gape mark and eye stripe is highly variable. All of the dark marks are more or less obscure in heavily spotted adults.

Adult size and intensity of spotting both vary geographically; therefore, body length at the onset of spotting also varies. Spots typically appear before the onset of puberty. The following is a description of the development of spotting to its extreme expression, as in some individuals from the Atlantic coast of the United States. Spots (dark gray to black) appear first in the gular and abdominal regions. Soon after appearance of dark ventral spots, light dorsal spots begin to develop. Both dark and light spots occur in the lateral field. The ventral spots enlarge and begin to coalesce, and the dorsal light spots spread ventrad, overlying the fused dark spots. Finally, the dorsal spots enlarge and coalesce in some areas, especially above the eyes, in the area of the spinal blaze and on the dorsal side of the peduncle. The light spots extend to the appendages. Portions of the original white ventral field remain uncovered in the gular and genital regions, peppered and bordered with dark spots. Thus, the most heavily spotted individuals appear uniformly dark gray with dorsal and ventral light spots and patches. The point to which the development of spots progresses varies both individually and geographically. Dolphins from the U.S. Atlantic coast, Gulf of Mexico and coasts of Central and South America have medium to heavy spotting (Figs. 1 and 8). In the Caribbean, they have medium spotting, with the underlying ground pattern clearly evident in mature adults (Fig. 1). Those from the offshore western North Atlantic (north of Cape Hatteras in the eastern extension of the Gulf Stream) have few if any spots (Fig. 10). This neotenoid coloration is correlated with small adult body size (described below). In the Azores, spotting is light to medium and the ventrum is typically unspotted (Fig. 10). On the coast of West Africa, spotting is again medium to heavy.

Minimum and maximum external dimensions and weights for cranially adult specimens (pmx fused to mx distally) are presented in Table 3. Maximum

→
Figure 10. Geographical variation in intensity of spotting in *Stenella frontalis*: A) unspotted cranially adult male (170 cm) from off Nova Scotia (EDM 786), B) lightly spotted subadult male (166 cm) from the Azores (AMNH 23911, EDM 761), C) and D) lateral and ventral views of a cranially adult female (175 cm) with medium dorsal and lateral spotting but white ventrum from the Azores (captured with B), E) a cranially adult female (179 cm) with lateral mixed dark and light spots, from off Venezuela (AMNH 239114). Heavily spotted condition illustrated in Fig. 8 and medium spotting in Fig. 1.

A



B



C



D



E



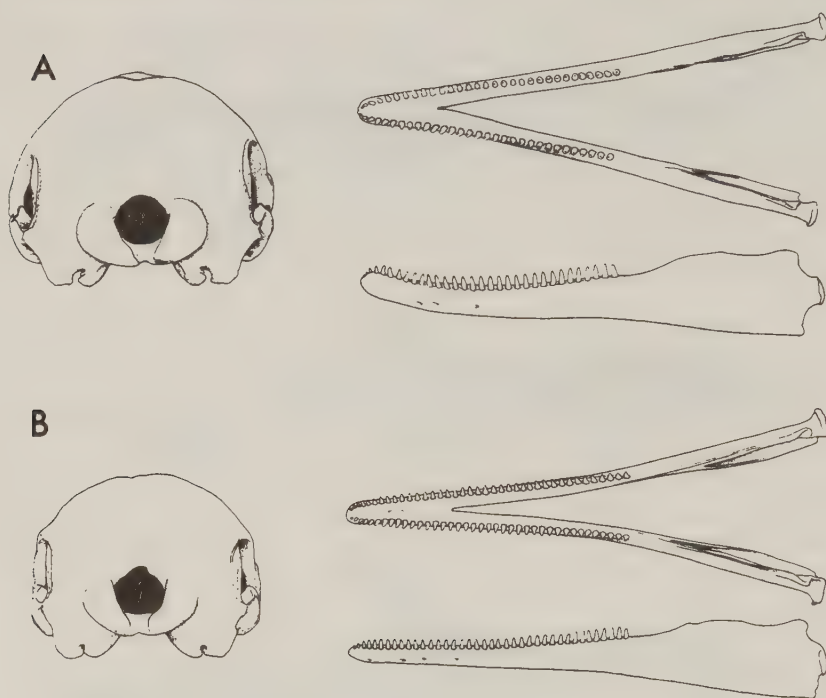


Figure 11. Typical adult skulls of A) *Stenella frontalis* (drawn from USNM 257833) and B) *S. attenuata* (drawn from R-1-SF), both from the Atlantic coast of Florida.

recorded length for males is 226 cm (a physically immature specimen from North Carolina; USNM 22017) and for females 229 cm (a specimen of unknown degree of physical maturity from Panama; USNM 254447). The smallest known cranially adult specimens were a 166-cm male (AMNH 239111 from the Azores, not physically mature) and a 167-cm female (UZMC *Prodelphinus* no. 2 from off Cape Verde, not physically mature). The smallest specimens known to have been physically mature were a 188-cm male from the Azores (UZMC *Prodelphinus* no. 4) and a 186-cm female from off Venezuela in the Caribbean (AMNH 239112). Geographical variation in size is discussed below.

A typical skull from the coastal western North Atlantic is illustrated in Figure 11. Ranges of skull measurements for cranially adult specimens and postcranial measurements for physically mature specimens are in Table 4. The largest known skull is of a 205-cm cranially immature male from off South Carolina (EDM 697). The smallest is of a 191-cm male from west of the Azores (UZMC *Prodelphinus* no. 11, CB length 356 mm). Ranges of the osteological measurements are not presented in Table 4 separately for males and females because many of the skulls in the overall sample are not identified to sex. In any case, the slight sexual dimorphism of the sort known for *Stenella attenuata* (Schnell

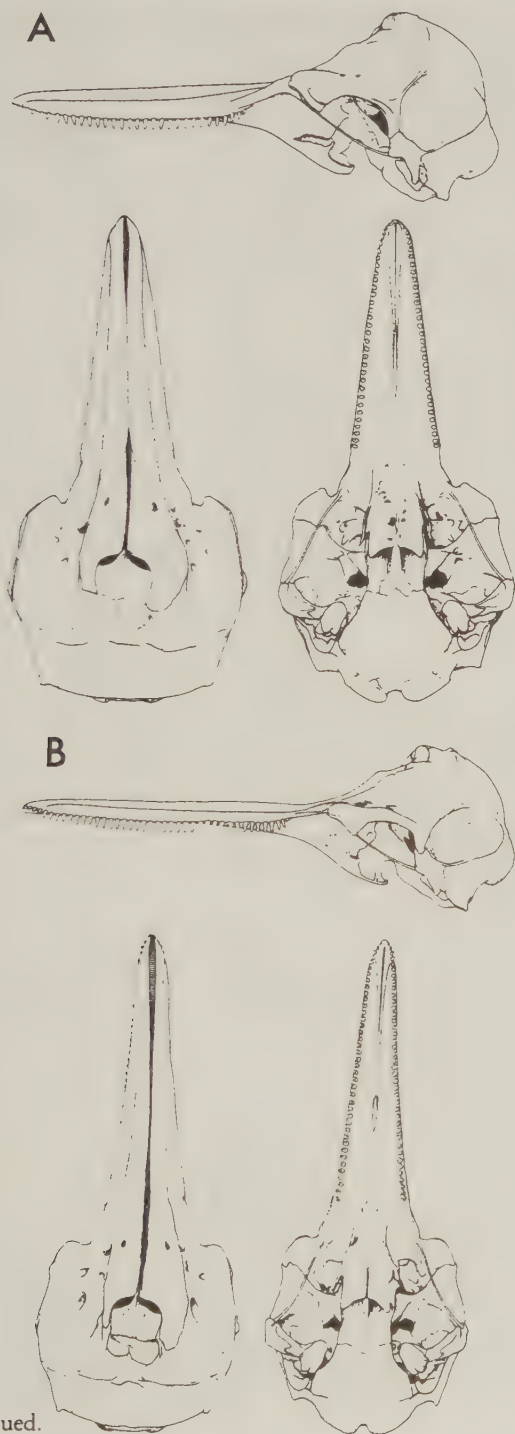


Figure 11. Continued.

Table 3. Minimum and maximum external dimensions (cm) and weights (kg) of cranially adult specimens of *Stenella frontalis* and *S. attenuata*. Males and females presented separately for measurements known to vary with sex in *S. attenuata* (Perrin 1975). Sample sizes in parentheses.

		<i>Stenella frontalis</i>	<i>Stenella attenuata</i>	
			Atlantic	All oceans
Total length	M	166-226 (33)	193-231 (6)	166-257 (>1,650)
	F	167-229 (46)	185-194 (4)	163-240 (>4,345)
Tip of upper jaw to:				
Apex of melon		9-14 (60)	9-12 (7)	8-13 (139)
Center of blowhole		23-35 (61)	28-32 (9)	24-33 (170)
Center of eye		25-35 (67)	29-32 (9)	25-33 (155)
End of gape		20-28 (58)	23-27 (7)	21-29 (161)
Ext. aud. meatus	M	30-39 (20)	36 (3)	31-37 (16)
	F	31-38 (31)	34-37 (3)	32-37 (18)
Ant. insert. of flip		38-53 (57)	40-45 (8)	34-45 (153)
Umbilical scar		81-105 (49)	87-103 (8)	80-107 (131)
Center of gen. slit	M	106-145 (24)	129-144 (3)	120-144 (16)
	F	112-158 (33)	130-133 (3)	124-162 (25)
Center of anus	M	119-162 (24)	140-166 (5)	135-166 (18)
	F	123-162 (39)	137-139 (3)	130-171 (25)
Tip of dorsal fin	M	100-137 (23)	113-118 (4)	100-120 (45)
	F	104-136 (39)	107-113 (3)	97-120 (83)
Girth at axilla	M	82-117 (22)	76-90 (3)	76-99 (42)
	F	82-111 (25)	79-85 (2)	71-94 (88)
Girth at anus	M	48-78 (22)	61-95 (4)	53-95 (18)
	F	47-72 (29)	49-56 (2)	49-66 (22)
Eye to:				
Ext. aud. meatus		5-7 (50)	5-6 (7)	5-7 (41)
End of gape		5-7 (54)	5-6 (6)	4-6 (29)
Center of blowhole		12-21 (51)	14-15 (6)	11-17 (109)
Flipper:				
		26-37 (57)	23-27 (9)	23-30 (32)
Ant. length		18-29 (55)	15-20 (8)	14-21 (121)
Post. length	M	9-14 (25)	8-12 (6)	8-12 (12)
Width	F	9-13 (34)	9-10 (3)	9-10 (15)
Flukes:				
Span		35-66 (64)	38-46 (8)	36-49 (120)
Width		10-17 (52)	10-13 (5)	10-15 (17)
Height of dorsal fin		16-25 (66)	13-17 (8)	12-20 (111)
Weight	M	50-143 (14)	87 (1)	max 119 kg
	F	39-127 (22)	— —	—

et al. 1985) could be expected to be negligible compared to the considerable geographic variation in skull size and shape. The series of specimens from the U.S. Atlantic coast and Gulf of Mexico is large enough to allow meaningful assessment of dimorphism (20 adult males and 35 adult females). In this series,

males and females differ in eight skull measurements and one postcranial measurement (t -test, at $\alpha = 0.05$): widths of the rostrum at 60 mm, $\frac{1}{2}$ length and $\frac{3}{4}$ length; width of the pmx's at $\frac{1}{2}$ length of the rostrum; postorbital, zygomatic and parietal widths; height of the braincase; and height of the first thoracic spine. Adult males are larger in all of these characters. Statistics for the several geographic series described below are presented separately for males and females for the dimorphic characters.

Tooth counts and postcranial meristics are presented in Table 5. Rostral tooth counts range from 32 to 42; lower counts range from 30 to 40. Total number of vertebrae ranges from 67 to 72; the typical formula is C7,T14,L17,Ca32 = 70.

Geographic variation—While very large portions of the range of the species are represented by only one or a very few specimens (e.g., the coasts of South America and Africa), some patterns of variation are evident or at least suggested by the available material. The analyses here are based on more or less coherent series from six geographic regions: (1) along the coast and over the continental shelf in the western North Atlantic coast and Gulf of Mexico; (2) the oceanic western North Atlantic (north of Cape Hatteras and east to 35° W in the eastern extension of the Gulf Stream); (3) the Azores; (4) the Caribbean (including some specimens from near the coast of Venezuela); (5) the mid-tropical Atlantic (including St. Helena); and (6) West Africa.

Adult body length is greatest along the western North Atlantic coast and in the Gulf of Mexico, averaging about 200–210 cm (Fig. 12). Very few data are available on adult length for the oceanic western North Atlantic and the Azores, but it would appear that adults there are about 20–30 cm smaller than adults from the coast to the west and south. Except for one specimen from Panama (229-cm female; USNM 254447), the Caribbean specimens were also smaller, centering around 180 cm. The sample from Africa is too small to allow interpretation, and there are no data on adult length available for the mid-tropical Atlantic.

There is marked geographic variation in the size and shape of the skull (Table 6). The skulls from the oceanic western North Atlantic and the Azores closely resemble skulls from the coastal western North Atlantic in shape but are very much smaller. This is correlated with the lesser body size and low-to-medium degree of spotting discussed above. The western North Atlantic coastal/Gulf of Mexico skulls are on the average larger than the Caribbean skulls in all measurements but one (prenarial width) for which sample sizes are large enough for meaningful comparison. The two series differ proportionately the most in rostral widths, dimensions of the temporal fossa and tooth width. The pelagic Caribbean animals have on the average a more slender rostrum, smaller temporal fossa and smaller teeth than do the coastal animals. As has been hypothesized for a similar coastal/pelagic difference in *Stenella attenuata* in the eastern Pacific (Perrin 1975), this may reflect differential feeding habits; the coastal form may feed on larger (perhaps demersal) prey than is taken by the pelagic form. The two series of skulls are least different in length of tooth row and other cranial dimensions that contain the tooth row.

Table 4. Minimum and maximum skull and postcranial skeletal measurements (mm) for *Stenella frontalis* and *S. attenuata*. Skull measurements are for cranially adult specimens; postcranial measurements are for physically mature specimens. Sample sizes in parentheses.

	<i>Stenella</i>		<i>Stenella attenuata</i>	
	<i>frontalis</i>	Atlantic	All oceans ^a	
Condylobasal length	356-461 (103)	369-437 (31)	356-460 (183)	
Length of rostrum	194-274 (105)	208-268 (31)	208-287 (176)	
Width of rostrum at base	76-107 (108)	80-95 (31)	74-100 (186)	
Width of rostrum at 1/2 length	55-82 (108)	55-70 (31)	46-77 (184)	
Width of pmx's at 1/2 length	44-63 (105)	39-49 (31)	35-60 (185)	
Width of rostrum at 3/4 length	22-36 (103)	19-28 (31)	17-32 (170)	
Rostrum tip to external nares	30-50 (105)	25-36 (31)	23-43 (177)	
Rostrum tip to internal nares	230-319 (105)	248-312 (31)	245-321 (182)	
Greatest preorb. width	236-329 (95)	257-320 (31)	243-329 (171)	
Greatest postorb. width	146-188 (106)	147-165 (31)	134-178 (184)	
Greatest width of ext. nares	165-210 (107)	165-185 (31)	151-196 (183)	
Zygomatic width	40-52 (105)	39-48 (31)	37-52 (175)	
Greatest width of pmx's	164-210 (107)	163-182 (31)	148-198 (183)	
Parietal width	65-87 (106)	64-73 (31)	57-76 (186)	
Height of braincase	130-171 (107)	130-150 (31)	129-161 (185)	
Int. length of braincase	93-121 (106)	89-109 (31)	87-113 (170)	
Length of temporal fossa	108-141 (105)	110-122 (31)	107-136 (160)	
Height of temporal fossa	57-89 (107)	58-73 (31)	53-97 (184)	
Length of orbit	45-72 (107)	43-59 (31)	33-79 (184)	
Length of preorb. process	45-60 (106)	45-53 (31)	43-59 (172)	
Width of internal nares	36-50 (105)	31-44 (31)	30-51 (173)	
Length of upper toothrow	40-59 (102)	46-54 (31)	40-61 (171)	
Length of lower toothrow	171-238 (104)	175-235 (30)	175-248 (180)	
	168-228 (99)	182-222 (31)	177-242 (175)	

Table 4. Continued.

	<i>Stenella attenuata</i>		
	<i>Stenella frontalis</i>	Atlantic	All oceans ^a
Length of ramus	292-399 (97)	312-375 (30)	296-393 (167)
Height of ramus	55-74 (97)	53-61 (30)	50-75 (170)
Diameter of tooth (at mid-length of lower row, transverse at alveolus)	3.2-5.3 (68)	3.0-4.1 (24)	2.6-4.1 (42)
Width of preauricular triangle at 60 mm	0.6-9.9 (93)	2.1-13.4 (28)	2.1-15.6 (160)
Atlas: width	68-97 (26)	73-83 (6)	73-90 (30)
height	49-60 (26)	45-49 (6)	46-61 (29)
length of lat. process	22-40 (26)	24-26 (6)	18-28 (29)
Length of last thor. neur. spine	72-98 (25)	73-81 (5)	55-81 (28)
First thor. vert.: height	30-57 (26)	42-45 (6)	44-60 (28)
width	75-98 (26)	72-79 (6)	63-86 (29)
First lumbar vert.: height	50-71 (25)	45-52 (6)	46-67 (28)
width	179-222 (25)	175-202 (6)	165-207 (28)
Length of first vert. rib	120-151 (26)	113-133 (6)	100-143 (29)
Length of longest vert. rib	242-314 (26)	234-286 (6)	232-313 (29)
Length of first stern. rib	75-99 (25)	73-84 (6)	66-88 (29)
Width of manubrium	88-112 (24)	73-94 (6)	63-106 (30)
Length of longest chev. bone	40-60 (23)	44-56 (6)	40-66 (26)
Scapula: height	116-155 (25)	105-127 (6)	101-135 (30)
length	113-143 (25)	109-132 (6)	99-132 (29)
Humerus: length	59-74 (16)	50-56 (6)	43-62 (30)
width	38-52 (22)	32-36 (6)	32-44 (30)
Length of radius	72-90 (22)	60-72 (6)	56-77 (30)
Length of ulna	66-80 (22)	54-61 (6)	48-65 (29)

^a From specimens listed below and from Perrin 1975, Perrin *et al.* 1979, Zhou *et al.* 1980, Ross 1984, Best 1969, Nishiwaki *et al.* 1965, Pinedo and Castello 1980.

Table 5. Statistics for meristic osteological characters for *Stenella frontalis* and *S. attenuata*. Standard deviations and coefficients of variation (CV) included for samples of 25 or more.

	<i>S. frontalis</i>										<i>S. attenuata</i>									
						Atlantic										All oceans				
	Range	Mean	SD	CV	N	Range	Mean	SD	CV	N	Range	Mean	SD	CV	N	Range	Mean	SD	CV	N
Tooth counts:	33-42	36.4	1.90	5.2	109	37-48	40.9	2.07	5.2	68	37-48	41.4	2.11	5.1	316					
	32-41	35.7	1.74	4.9	109	35-47	40.3	2.12	5.3	67	35-47	40.6	2.08	5.1	315					
	31-40	34.8	2.25	6.5	103	36-45	39.9	2.10	5.3	69	34-47	40.4	2.04	5.0	315					
	30-40	34.1	2.29	6.7	101	35-45	39.3	1.92	4.9	69	34-45	39.6	1.99	5.0	315					
Vertebrae:	67-72	70.0	1.07	1.5	52	74-81	79.3	—	—	—	9	74-84	79.7	1.55	1.9	175				
	13-15	14.2	0.47	3.3	46	14-16	15.1	—	—	—	9	13-17	15.8	0.73	4.6	184				
	15-20	17.0	1.19	7.0	30	17-23	20.3	—	—	—	7	17-24	19.8	1.45	7.3	154				
	28-35	31.8	1.65	5.2	32	34-41	36.4	—	—	—	7	32-42	37.0	1.65	4.5	155				
	45-51	48.0	1.23	2.6	49	52-59	56.0	—	—	—	9	52-61	56.6	1.74	3.1	125				
	50-55	53.0	0.90	1.7	49	56-62	60.4	—	—	—	9	56-66	62.3	1.45	2.3	123				
	56-60	58.1	0.96	1.7	49	61-68	66.1	—	—	—	8	61-71	67.6	1.44	2.1	120				
	38-41	39.0	0.90	2.3	28	41-46	43.5	—	—	—	6	41-47	43.5	1.40	3.2	94				
	60-65	62.2	1.43	2.3	25	66-72	70.0	—	—	—	5	66-77	72.1	1.63	2.3	85				
	21-26	23.9	—	—	21	26-33	27.4	—	—	—	5	24-33	29.7	1.74	5.9	73				
	1-3	2.2	0.67	30.4	31	2-3	2.7	—	—	—	6	0-3	1.8	0.51	28.3	118				
	digit 1, highest no. of phalanges																			
Manus: ^b	II	7-10	8.7	0.78	9.0	31	9-10	9.4	—	—	5	7-10	8.5	0.70	8.2	110				
	III	6-8	6.7	0.55	8.2	30	6-7	6.4	—	—	5	4-7	6.1	0.55	9.0	110				
	IV	2-4	3.1	0.53	17.1	29	3	3.0	—	—	5	2-4	2.9	0.48	16.6	105				
	V	0-2	1.5	0.63	42.0	30	2	2.0	—	—	5	0-2	1.6	0.37	23.1	105				
	carp. & metacarp., highest number	4-7	5.3	0.65	12.3	31	5-6	5.5	—	—	6	5-8	6.2	—	—	131				

^a Equals highest vertebral rib count.

^b Some variation in phalanges may be caused by confusion with metacarpals (as pointed out by True 1894).

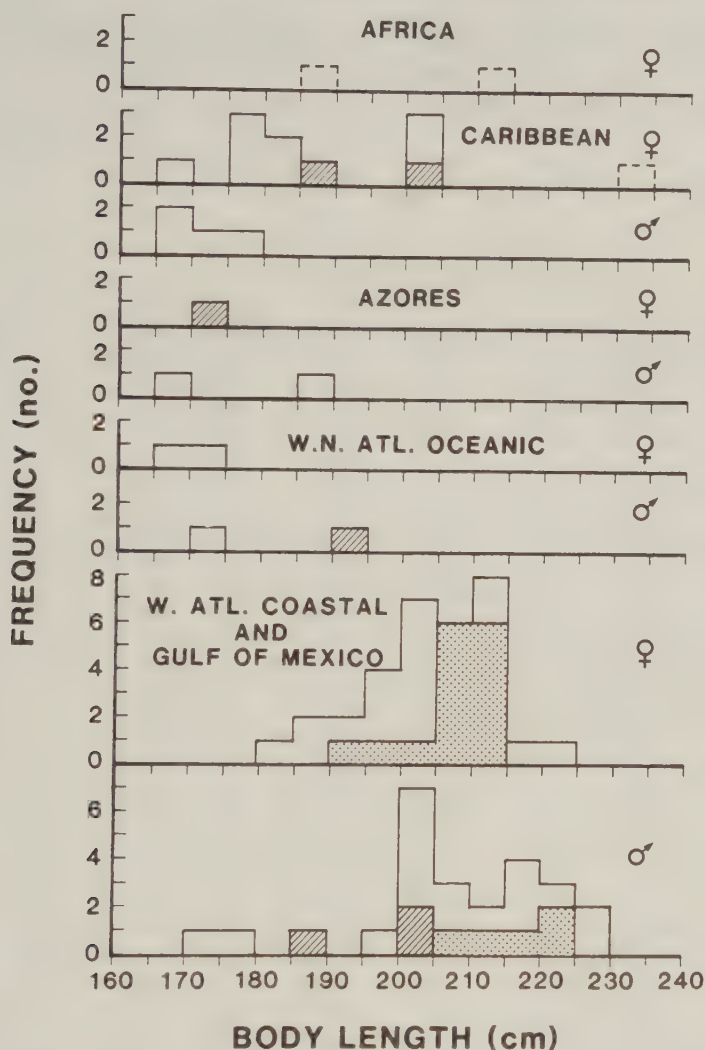


Figure 12. Frequency distributions of body length for five geographical samples of cranially adult specimens of *Stenella frontalis*. Shaded portions represent physically mature specimens; dashed portions are specimens of unknown degree of physical maturity.

The largest Caribbean skull (USNM 254447) was collected on the coast of Panama (inside the 100-fathom [183-m] curve). Spotted dolphins along the coast of Central America may be larger than animals in the Caribbean proper to the east.

The western North Atlantic coastal form is also larger in all postcranial skeletal dimensions, the differences being greatest for the transverse processes of the vertebrae, the sternum and the scapula. The bones of the manus show

Table 6. Statistics for skull and postcranial measurements (mm) of geographical series of *Stenella frontalis*. Standard deviations included for samples ≥ 25 . Characters showing sexual dimorphism (t -test, M or F sample ≥ 25 , $\alpha = 0.05$) presented separately for males

A						
N.W. Atlantic Coast & Gulf of Mexico						
		Range	(n)	Mean	SD	CV
Condylobasal length		396-461	(62)	427.6	15.37	3.59
Length of rostrum		222-274	(63)	247.2	11.82	4.78
Width of rostrum at base		86-107	(66)	96.9	4.53	4.67
Width of rostrum at 60 mm	M	67-78	(20)	72.4	—	—
	F	60-82	(35)	69.5	3.91	5.63
Width of rostrum at ½ length	M	53-63	(20)	57.8	—	—
	F	48-63	(34)	55.9	3.48	6.23
Width of pmx's at ½ length	M	27-35	(20)	31.2	—	—
	F	24-34	(34)	29.5	2.65	8.98
Width of rostrum at ¾ length	M	38-50	(20)	43.7	—	—
	F	34-48	(34)	41.2	3.11	7.55
Rostrum tip to external nares		260-319	(63)	289.0	12.86	4.45
Rostrum tip to internal nares		264-329	(59)	295.5	13.93	4.71
Greatest preorb. width		160-188	(65)	176.8	6.16	3.48
Greatest postorb. width	M	187-210	(20)	201.3	—	—
	F	183-207	(35)	197.9	6.17	3.12
Greatest width of ext. nares		41-52	(65)	46.5	2.24	4.82
Zygomatic width	M	185-210	(20)	201.5	—	—
	F	184-208	(35)	196.7	6.10	3.10
Greatest width of pmx's		70-87	(65)	78.6	3.52	4.48
Parietal width	M	141-171	(20)	157.5	—	—
	F	141-164	(35)	153.3	4.99	3.26
Height of braincase	M	103-118	(20)	112.4	—	—
	F	100-120	(35)	109.1	4.49	4.12
Int. length of braincase		114-141	(65)	129.6	4.74	3.66
Length of temporal fossa		61-89	(66)	79.3	4.99	6.29
Height of temporal fossa		45-72	(66)	60.7	4.87	8.02
Length of orbit		50-60	(65)	55.9	2.33	4.17
Length of preorb. process		39-50	(65)	44.4	2.62	5.90
Width of internal nares		46-59	(62)	53.1	2.94	5.54
Length of upper toothrow		191-238	(63)	211.7	10.31	4.87
Length of lower toothrow		181-228	(59)	205.7	9.90	4.81
Length of ramus		332-399	(59)	365.6	14.68	4.02
Height of ramus		61-75	(58)	68.3	3.20	4.69
Diameter of tooth (at mid-length of lower row, transverse at alveolus)		3.5-5.3	(39)	4.50	0.390	8.67
Width of prenasial triangle at 60 mm		0.6-7.3	(54)	3.77	1.834	48.65
Atlas: width		79-98	(27)	87.7	4.21	4.80
height		52-60	(29)	55.3	2.13	3.85
length of lat. process		25-40	(29)	30.1	3.89	12.92

and females (except specimens from mid-tropical Atlantic, which are of unknown sex and are compared to the pooled sexes for series A).

B N.W. Atlantic Oceanic				C Azores			
Range	(n)	Mean	Com- pari- son of A and B	Range	(n)	Mean	Com- pari- son of A and C
356-393	(5)	374.6	***	375-384	(3)	380.3	***
194-229	(6)	215.5	***	211-221	(3)	215.3	***
83-88	(6)	85.5	***	81-85	(3)	82.3	***
61-64	(2)	62.5	—	59-60	(2)	59.5	—
61-64	(4)	63.3	**	60	(1)	60.0	*
48-50	(2)	49.0	—	47-50	(2)	48.5	—
47-54	(4)	50.5	**	48	(1)	48.0	*
26-28	(2)	27.0	—	27	(2)	27.0	—
26-31	(4)	28.5	ns	26	(1)	26.0	ns
32-36	(2)	34.0	—	33-38	(2)	35.5	—
32-37	(4)	34.8	***	34	(1)	34.0	*
230-263	(6)	250.5	***	245-256	(3)	250.3	***
236-277	(4)	254.5	***	258-268	(3)	261.7	***
155-162	(5)	157.6	***	150-160	(3)	156.0	***
173-177	(2)	175.0	—	179-181	(2)	180.0	—
175-182	(3)	177.7	***	177	(1)	177.0	*
44-46	(5)	45.4	ns	43-47	(3)	45.0	ns
172-178	(2)	175.0	—	180-183	(2)	181.5	—
172-182	(3)	176.3	***	179	(2)	179.0	**
65-75	(5)	70.6	***	71-72	(3)	71.3	***
141-144	(2)	142.5	—	146	(2)	146.0	—
137-144	(3)	140.7	***	137	(1)	137.0	**
100-101	(2)	100.5	—	102-109	(2)	105.5	—
97-104	(3)	100.7	**	97	(1)	97.0	*
108-118	(5)	114.4	***	114-126	(3)	118.3	***
68-71	(5)	69.2	***	65-68	(3)	66.7	***
46-56	(5)	52.2	***	46-55	(3)	51.0	**
45-51	(6)	48.5	***	47-52	(3)	50.0	***
37-45	(6)	40.0	***	40	(3)	40.0	***
48-52	(5)	49.8	**	47-49	(3)	48.0	**
171-200	(6)	186.2	***	183-188	(3)	185.3	***
168-197	(6)	181.7	***	180-184	(3)	181.7	***
292-332	(6)	315.8	***	315-324	(3)	319.7	***
56-61	(6)	58.5	***	56-61	(3)	59.0	***
3.8-4.3	(6)	4.08	**	3.2-3.8	(3)	3.57	**
3.1-5.2	(6)	3.92	ns	1.8-2.7	(3)	2.13	ns
74-82	(5)	77.6	***	76-79	(3)	77.7	***
48-51	(5)	49.0	***	49-52	(3)	50.3	**
20-28	(5)	23.0	***	22-25	(3)	23.7	**

Table 6. Continued.

A					
N.W. Atlantic Coast & Gulf of Mexico					
	Range	(n)	Mean	SD	CV
Length of last thor. neur. spine	72-98	(27)	83.6	6.30	7.54
First thor. vert.: height	30-57	(29)	49.0	5.35	10.92
width	77-98	(29)	88.6	5.97	6.74
First lumbar vert.: height	43-71	(28)	55.6	4.89	8.79
width	184-222	(28)	202.9	9.83	4.84
Length of first vert. rib	120-151	(29)	136.8	8.40	6.14
Length of longest vert. rib	253-314	(29)	291.3	15.5	5.32
Length of first stern. rib	74-99	(28)	87.8	5.25	5.98
Width of manubrium	80-112	(27)	103.4	6.89	6.66
Length of longest chev. bone	41-60	(26)	51.9	5.68	10.94
Scapula: height	110-155	(28)	139.1	9.86	7.09
length	99-143	(28)	128.7	10.53	8.18
Humerus: length	62-74	(23)	67.7	—	—
width	39-52	(25)	43.8	3.54	8.08
Length of radius	77-95	(25)	83.9	4.41	5.26
Length of ulna	67-84	(25)	74.6	4.37	5.86
D					
Caribbean					
	Range	(n)	Mean	t-test ^a	Comparison of D and A Percent difference
Condylbasal length	374-431	(17)	398.3	***	6.85
Length of rostrum	211-261	(17)	233.8	***	5.42
Width of rostrum at base	76-93	(17)	85.9	***	11.35
Width of rostrum at 60 mm	M 59-67	(4)	62.3	—	—
	F 55-69	(11)	62.1	***	10.65
Width of rostrum at 1/2 length	M 48-53	(4)	50.3	—	—
	F 44-53	(11)	48.7	***	12.88
Width of pmx's at 1/2 length	M 24-30	(4)	27.5	—	—
	F 23-30	(11)	26.7	**	9.49
Width of rostrum at 3/4 length	M 35-38	(4)	36.8	—	—
	F 30-39	(11)	34.7	***	15.78
Rostrum tip to external nares	247-303	(17)	273.1	***	5.50
Rostrum tip to internal nares	259-311	(16)	280.1	***	5.21
Greatest preorb. width	146-172	(17)	159.9	***	9.56
Greatest postorb. width	M 166-189	(4)	177.0	—	—
	F 165-194	(11)	181.0	***	8.54
Greatest width of ext. nares	40-47	(16)	42.9	***	7.96

Table 6. Extended.

B N.W. Atlantic Oceanic				C Azores			
Range	(n)	Mean	Com- pari- son of A and B	Range	(n)	Mean	Com- pari- son of A and C
65-82	(5)	73.4	**	73-75	(2)	74.0	*
40-47	(5)	43.0	*	43-45	(3)	43.7	ns
71-87	(5)	77.6	***	76-81	(3)	78.7	**
45-53	(5)	47.6	**	45-50	(2)	47.5	*
169-192	(5)	181.2	***	177-179	(2)	178.0	**
107-132	(5)	117.6	***	110-127	(3)	120.7	**
223-243	(5)	236.0	***	234-245	(3)	240.3	***
72-89	(5)	78.2	***	75-80	(3)	78.0	**
73-99	(5)	84.8	***	88-92	(3)	89.7	**
41-50	(5)	44.8	*	40-49	(3)	44.7	*
109-127	(5)	118.2	***	116-123	(3)	119.0	**
96-131	(5)	109.6	**	113-115	(3)	114.3	*
55-60	(3)	58.0	***	57-59	(2)	58.0	**
35-40	(5)	36.8	**	36-38	(3)	37.3	*
69-76	(5)	72.4	***	72-77	(2)	74.5	**
58-72	(5)	64.0	***	66-69	(2)	67.5	*

E Mid-Tropical Atlantic				F Africa			
Range	(n)	Mean	Com- pari- son of A and E	Range	(n)	Mean	Com- pari- son of A and F
382-406	(3)	390.7	***	368-419	(9)	396.2	***
220-232	(3)	226.3	**	212-248	(9)	230.3	***
81-86	(3)	84.3	***	81-93	(9)	87.1	***
55-62	(3)	59.3	***	67	(1)	67.0	—
				62-70	(2)	66.0	ns
45-48	(3)	46.7	***	56	(1)	56.0	—
				51-55	(2)	53.0	ns
22-27	(3)	24.7	***	30	(1)	30.0	—
				25-33	(2)	29.0	ns
33-35	(3)	33.7	***	38	(1)	38.0	—
				37-41	(2)	39.0	ns
253-272	(3)	262.7	***	249-289	(9)	269.0	***
263-288	(3)	274.7	*	262-297	(8)	279.8	**
150-160	(3)	156.3	***	153-170	(9)	163.3	***
169-179	(3)	175.3	***	188	(1)	188.0	—
				183-188	(2)	185.5	*
43-46	(3)	45.0	ns	42-48	(9)	45.2	ns

Table 6. Continued.

		D Caribbean				Per- cent dif- fer- ence
		Range	(n)	Mean	t- test ^a	
Zygomatic width	M	167-184	(4)	174.8	—	—
	F	164-194	(11)	180.2	***	8.39
Greatest width of pmx's		66-78	(17)	71.3	***	9.29
Parietal width	M	131-151	(4)	140.8	—	—
	F	133-151	(11)	142.0	***	7.37
Height of braincase	M	96-106	(4)	100.0	—	—
	F	93-106	(11)	98.3	**	9.90
Int. length of braincase		108-124	(16)	117.5	***	9.34
Length of temporal fossa		57-80	(17)	69.8	***	11.98
Height of temporal fossa		48-62	(17)	54.5	***	10.21
Length of orbit		47-56	(16)	51.4	***	8.05
Length of preorb. process		36-47	(16)	40.9	***	7.88
Width of internal nares		40-55	(16)	48.5	***	8.66
Length of upper toothrow		179-227	(17)	202.8	**	4.20
Length of lower toothrow		184-224	(15)	196.0	**	4.72
Length of ramus		316-372	(15)	337.8	***	7.60
Height of ramus		55-66	(16)	60.4	***	11.57
Diameter of tooth (at mid-length of lower row, transverse at alveolus)		3.3-4.6	(13)	3.94	***	12.44
Width of prenarial triangle at 60 mm		1.0-6.8	(16)	3.23	ns	—
Atlas: width		76-82	(10)	79.8	***	9.01
height		46-54	(10)	49.2	***	11.03
length of lat. process		19-27	(10)	22.4	***	25.48
Length of last thor. neur. spine		62-80	(10)	71.7	***	14.23
First thor. vert.: height		39-48	(9)	44.7	**	8.78
width		66-90	(10)	76.6	**	13.50
First lumbar vert.: height		44-51	(10)	47.7	***	14.21
width		158-207	(10)	175.2	***	13.65
Length of first vert. rib		107-133	(10)	116.0	***	15.20
Length of longest vert. rib		200-274	(10)	244.5	***	16.07
Length of first stern. rib		68-92	(10)	77.0	***	12.30
Width of manubrium		72-92	(10)	83.3	***	19.44
Length of longest chev. bone		38-54	(10)	43.2	***	16.76
Scapula: height		102-138	(8)	115.8	***	16.75
length		88-123	(8)	105.3	***	18.18
Humerus: length		54-62	(4)	57.0	—	—
width		35-42	(9)	39.1	**	10.73
Length of radius		70-82	(9)	74.9	***	10.73
Length of ulna		60-73	(9)	67.6	***	9.38

^a A t-test, based on pooled variance (homogeneity assumed); ns, $P < 0.05$; *, $0.05 \leq P < 0.01$; **, $0.01 \leq P < 0.001$; ***, $P \leq 0.001$. Blank indicates that larger sample < 25.

Table 6. Extended.

E Mid-Tropical Atlantic				F Africa			
Range	(n)	Mean	Com- pari- son of A and E	Range	(n)	Mean	Com- pari- son of A with F
167-179	(3)	175.0	***	189	(1)	189.0	—
				184-186	(2)	185.0	*
66-73	(3)	69.0	***	68-76	(9)	72.7	***
130-149	(3)	142.0	***	140	(1)	140.0	—
				143-152	(2)	147.5	ns
94-103	(3)	99.3	***	97	(1)	97.0	—
				102-105	(2)	103.5	ns
111-121	(3)	116.7	***	112-131	(9)	122.4	***
67-69	(3)	68.0	***	67-74	(9)	70.4	***
53-59	(3)	56.7	ns	47-61	(9)	54.4	***
48-50	(3)	49.3	***	47-54	(9)	50.4	***
39-45	(3)	41.3	ns	37-46	(8)	41.4	**
44-53	(3)	49.0	*	46-56	(8)	49.9	**
187-203	(3)	193.6	**	118-216	(9)	198.1	***
178-197	(3)	186.0	**	181-209	(8)	195.3	**
321-345	(3)	329.3	***	316-352	(8)	335.1	***
58-61	(3)	59.0	***	56-66	(8)	60.0	***
3.3-3.5	(3)	3.37	***	35-38	(2)	36.5	**
1.5-2.1	(3)	1.90	ns	0.8-9.9	(8)	3.64	ns
74	(1)	74.0	*	—	—	—	—
45	(1)	45.0	***	—	—	—	—
17	(1)	17.0	**	—	—	—	—
64	(1)	64.0	**	—	—	—	—
44	(1)	44.0	ns	—	—	—	—
70	(1)	70.0	**	—	—	—	—
43	(1)	43.0	*	—	—	—	—
168	(1)	168.0	**	—	—	—	—
109	(1)	109.0	**	—	—	—	—
221	(1)	221.0	***	—	—	—	—
74	(1)	74.0	*	—	—	—	—
66	(1)	66.0	***	—	—	—	—
37	(1)	37.0	*	—	—	—	—
109	(1)	109.0	**	—	—	—	—
90	(1)	90.0	**	—	—	—	—
59	(1)	59.0	*	—	—	—	—
37	(1)	37.0	ns	—	—	—	—
69	(1)	69.0	**	—	—	—	—
62	(1)	62.0	**	—	—	—	—

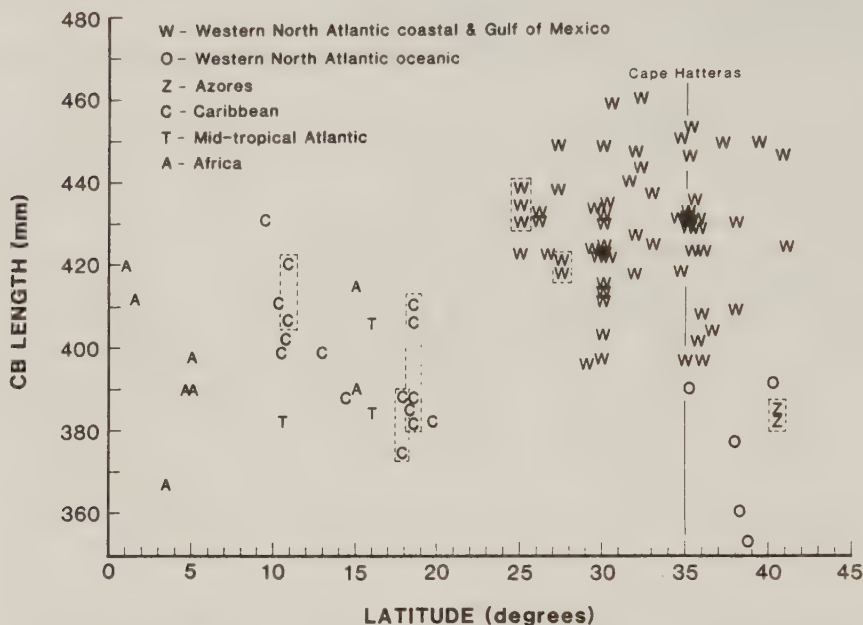


Figure 13. Scatterplot of CB length on latitude (absolute) for six geographical series of *Stenella frontalis*. Specimens enclosed in dashed rectangles captured or stranded together.

less difference in size between the two series than do nearly all of the other postcranial elements, although the differences are large relative to those in most of the skull characters.

The specimens from the mid-tropical Atlantic are also smaller than the coastal specimens in nearly all cranial and postcranial dimensions. The African series appears intermediate; the specimens came from localities scattered from Cape Verde to the eastern Gulf of Guinea, and it is possible that more than one population is involved. For example, the specimens from the Cape Verde Islands could be from an oceanic population and others from one or more coastal populations.

The variation in skull size exhibits a latitudinal pattern (Fig. 13). The Caribbean offshore and mid-tropical Atlantic specimens form a group of smaller skulls from between 10° and 20° (north and south) (but note the 431-mm skull from Panama), and the western North Atlantic oceanic and Azores series comprise a group of very small high-latitude skulls, all smaller than any other skulls from north of 20°N. This reflects the apparent circular distribution in the Atlantic (Fig. 7), with coastal animals at mid-latitudes and small oceanic animals at low and high latitudes. The circular pattern of distribution could be an artifact of sampling effort.

In a factor analysis based on 22 skull measurements considered simultaneously (Table 7), the several series exhibit a similar pattern (Fig. 14). The

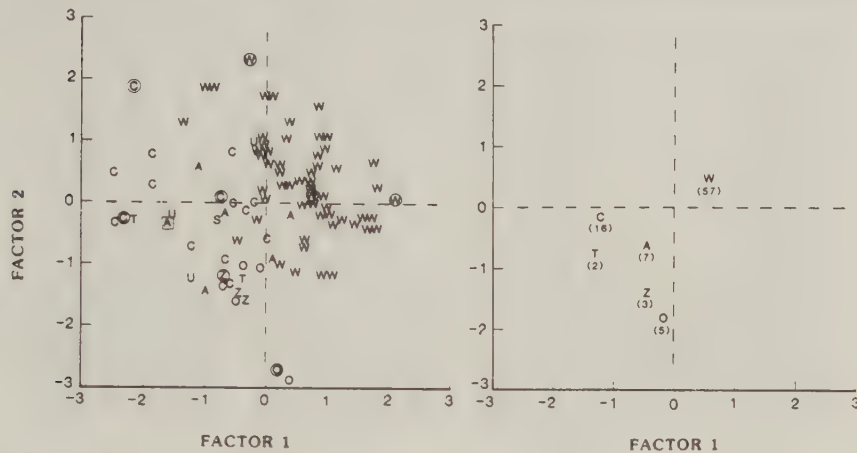


Figure 14. (Left) Skulls of six geographical samples of *Stenella frontalis* plotted on first two orthogonally rotated factors. U = unknown locality; see Figure 13 for other symbols. Holotype (from Africa) in box. Circled specimens illustrated in Figure 15. (Right) Group means of the geographical series.

Table 7. Loadings of orthogonally rotated factors for 22 skull measurements of 94 specimens of *Stenella frontalis*. Factors sorted so that variables appear in decreasing order of variance explained by factors. Rearranged so that for each successive factor, loadings greater than 0.5000 appear first. Loading less than 0.25 indicated by dash. Proportion of total variance explained by Factors 1 and 2 = 0.79.

	Component	
	I	II
Width of rostr. at 60 mm	0.846	0.414
Width of rostr. at 1/2 length	0.835	0.374
Width of rostr. at 3/4 length	0.820	0.425
Width of rostr. at base	0.810	0.459
Zygomatic width	0.807	0.540
Width of pmx's at 1/2 length	0.803	—
Postorbital width	0.796	0.555
Preorbital width	0.765	0.569
Width of int. nares	0.762	—
Height of braincase	0.748	0.431
Parietal width	0.707	0.476
Greatest width of pmx's	0.692	—
Int. length of braincase	0.640	0.600
Greatest width of ext. nares	0.639	—
Length of temporal fossa	0.619	0.597
Length of preorb. process	0.580	0.474
Length of rostrum	0.271	0.939
Length of upper toothrow	—	0.919
Rostr. tip to external nares	0.324	0.917
Condylbasal length	0.482	0.863
Length of orbit	0.458	0.737
Height of temporal fossa	0.481	0.587

loadings for Factor 1 are highest (and account for most of the variance) for the measurements that involve skull widths (*i.e.*, the rostral widths, facial widths and cranial widths), while they are highest for Factor 2 for the length measurements (CB, rostral and tooth-row lengths, *etc.*). The western North Atlantic skulls are both long and relatively broad, the skulls from the offshore western North Atlantic, the Azores and the mid-tropical Atlantic are small and relatively broad, and the Caribbean skulls are of intermediate size and narrow (Fig. 14). The African sample is heterogeneous but closest to the Caribbean sample. Specimens at or near the extreme values for the two factors and modal specimens for the western North Atlantic coastal series, the Caribbean series and the (small) series from the Azores are illustrated in Figure 15.

There is significant geographical variation in number of teeth; the range of the series means is 3 or 4 teeth in each jaw, or 12–16 overall. Tooth counts are lowest in the western North Atlantic coastal series and the specimens from the Azores (Table 8). The mid-tropical Atlantic specimens have the highest counts, and the western North Atlantic oceanic, Caribbean and African series are intermediate.

There is little geographical variation in postcranial meristic characters (Table 8). Total number of vertebrae is remarkably constant ($CV = 1.40$). Only the positions of the first vertebra with a vertically perforating foramen and the last vertebra with a neural process vary among the series; the values for the former are greater in the western North Atlantic oceanic and Caribbean series and the latter greater in the Caribbean series than in the western North Atlantic coastal series.

Comparisons—*Stenella frontalis* differs in coloration from the other spotted dolphin, *S. attenuata*, in having a spinal blaze and lacking a division of the peduncle into upper dark and lower light halves. The background of dark ventral spots is white, rather than gray as in *S. attenuata*. The ground pattern is very similar to that of the bottlenose dolphin *Tursiops truncatus* (Montagu); similar features are broad and complex eye and blowhole stripes, flipper stripe demarcated dorsally by a narrow light line, flipper stripe terminating anteriorly at the eye or between the eye and the angle of the gape (in most specimens of *S. frontalis*), ventral margin of dorsal cape interrupted by spinal blaze, and ventral margin of lateral field terminating in the anal region. The two species differ materially only in possession of dorsal spots (some geographical forms of *T. truncatus* have dark ventral spots—Ross 1977).

Length at birth in *S. frontalis* is between 76 and 120 cm (Caldwell and Caldwell 1966, Perrin and Reilly 1984). The range of adult body length is about the same as in *S. attenuata* (although that species may reach a greater length; Table 3), but *S. frontalis* is heavier bodied (Fig. 16). Adults of the same length weigh 10 to 30 kg more. *Stenella frontalis* also has larger flippers, flukes and dorsal fins (Table 3). In external size and shape, it is intermediate between *S. attenuata* and *T. truncatus*, showing many similarities to the latter in external morphology of the rostrum, melon, flippers and dorsal fin (Fig. 17). Again, the similarity to *T. truncatus* is greatest for the spotted form of that

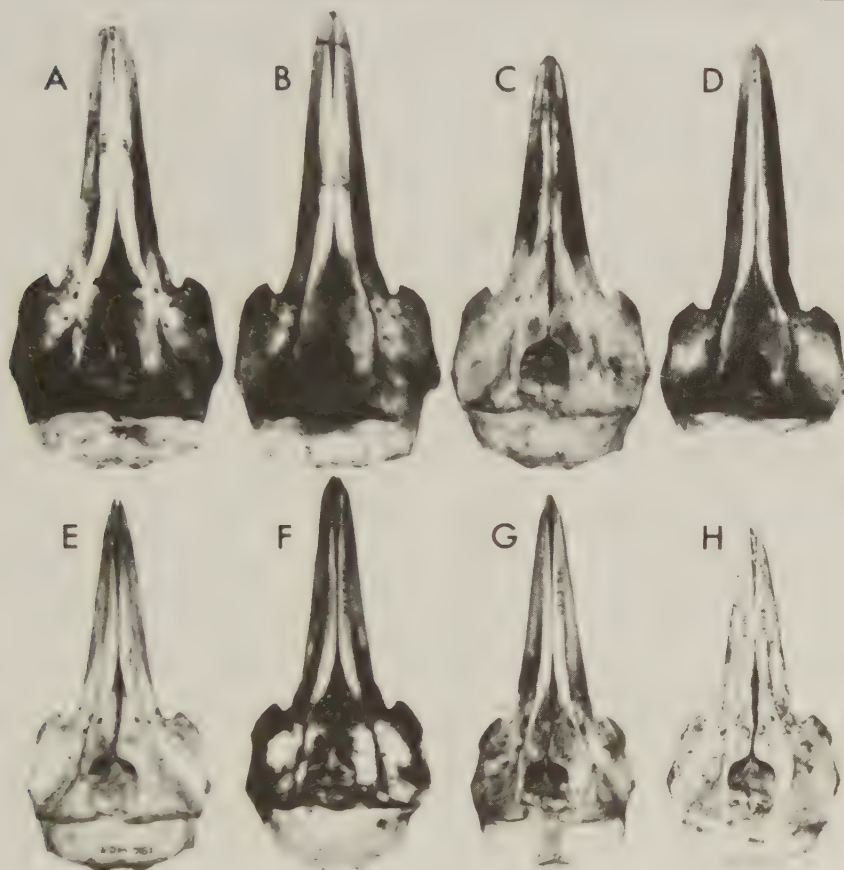


Figure 15. Variation in adult skull size and shape in *Stenella frontalis* (specimens circled in Fig. 14). A) MCZ 1182, sex unknown, South Carolina (western North Atlantic specimen—"C" in Fig. 14, factor scores 2.10, 0.14); B) USNM 21915, sex unknown, Florida Gulf Coast ("W": -0.32, 2.35); C) EDM 694, female, North Carolina ("W": 0.75, 0.03); D) USNM 254447, female, coast of Panama ("C": -0.07, 1.86); E) AMNH 239111 (= EDM 761), male, Azores ("Z": -0.64, -1.16); F) UF VI-2-SF, sex unknown, Virgin Islands ("C": -0.74, 0.10); G) UF VI-3-SF, sex unknown, Virgin Islands—stranded with UF VI-2-SF ("C": -2.29, -0.26); H) MCZ 51073, female, off New Jersey ("O": 0.11, 2.75).

species, which has a proportionately slimmer rostrum than do the unspotted forms (Ross 1977).

Stenella frontalis shares with *S. attenuata* and *T. truncatus* a suite of cranial characters that separate the three species from the other small delphinids with dorsal fin and externally well-defined beak (abrupt transition from beak to melon) (i.e., *S. longirostris*, *S. clymene*, *S. coeruleoalba*, *Delphinus delphis* and

Table 8. Continued.

	D Caribbean			E Mid-tropical Atlantic			F Africa		
	Range	(n)	Mean	Range	(n)	Mean	Range	(n)	Mean
Tooth counts:									
Highest rostral	35-41	(17)	37.7	39-40	(3)	39.3	36-42	(10)	37.6
Lowest rostral	34-41	(17)	37.0	37-39	(3)	38.0	36-39	(10)	36.7
Highest mandibular	34-40	(15)	36.6	38	(3)	38.0	36-40	(9)	37.3
Lowest mandibular	34-39	(15)	36.3	37-38	(3)	37.3	34-40	(9)	36.3
Vertebrae:									
Total number	69-72	(10)	70.3	70	(1)	70.0	68-70	(2)	69.0
Thoracic	14-15	(10)	14.3	14	(1)	14.0	—	—	—
First with vert. for.	48-50	(10)	48.8	48	(1)	48.0	49	(1)	49.0
Last with trans. proc.	53-54	(10)	53.3	54	(1)	54.0	53	(1)	53.0
Last with neur. proc.	58-60	(10)	58.9	58	(1)	58.0	58	(1)	58.0

^a A *t*-test based on pooled variance; ns, $P > 0.05$; *, $0.05 \leq P < 0.01$; **, $0.01 \leq P < 0.001$; ***, $P \leq 0.001$.

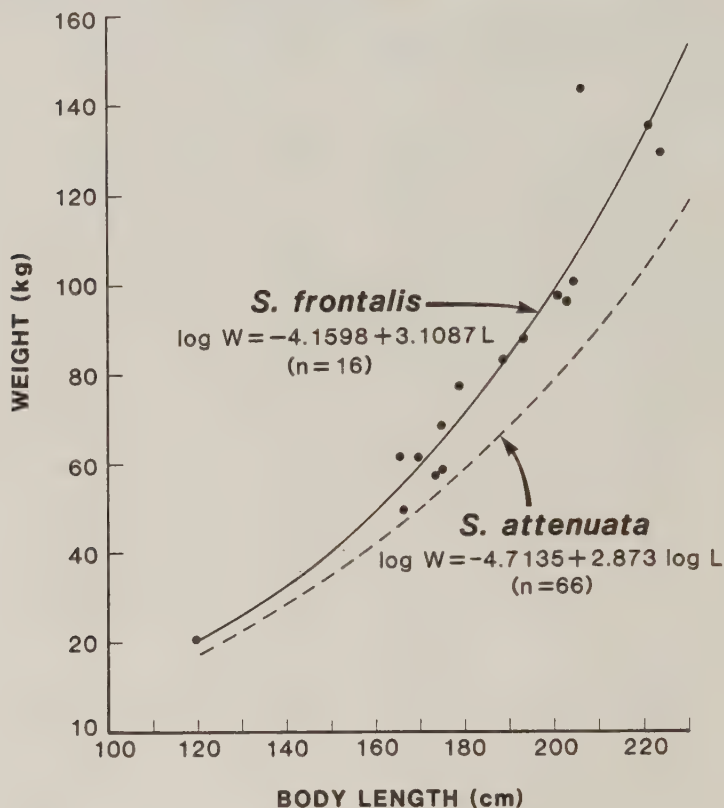


Figure 16. Length-weight relationships for males of *Stenella frontalis* and *S. attenuata* (from Perrin *et al.* 1976).

Lagenodelphis bosei; Perrin *et al.* (1981): (1) a relatively large temporal fossa; (2) typically about 40 or fewer teeth in each row; (3) well developed alveoli in the distal 1 cm or so in upper and lower jaws; (4) proximal halves of upper and lower tooth rows convergent in a continuous curve rather than in a sigmoid curve; (5) a relatively long mandibular symphysis; (6) distal half of the rostrum not markedly flattened dorso-ventrally; and (7) no grooves in the palate. *S. frontalis* and *S. attenuata* overlap in all skull characters, but in the former the rostrum is on the average broader distally, the preauricular triangle shorter and the teeth larger and less numerous. In large specimens, the tip of the mandible usually curves upward (Fig. 11), but in small specimens (*e.g.*, those from the offshore western North Atlantic) it may be straight, as in *S. attenuata*. Large skulls of *S. frontalis* from some regions are similar to small skulls of *T. truncatus* but can be separated from them on the basis of tooth count (more than 30 in each row in *S. frontalis*).

As well as differing in minimum and maximum values for nearly all post-



Figure 17. A young specimen of *Stenella frontalis* (top) and a specimen of *Tursiops truncatus*, showing similarities in ground coloration and shape of rostrum and melon.

cranial measures (those for *S. frontalis* being greater), *S. frontalis* and *S. attenuata* are distinct in some of the characters. The present series of physically mature adult specimens ($n = 22$ and 29 , respectively) do not overlap in length of the ulna, and the overlap in length of radius is very slight (Table 4); the osseous flipper in *S. frontalis* is proportionately longer. The two species are also separate in vertebral counts; *S. frontalis* typically has one or two fewer thoracic vertebrae (and ribs), three fewer lumbar and five or six fewer caudals than does *S. attenuata*, for totals of $67-72$ and $74-84$ in the two species, respectively (Table 5). *T. truncatus* has 65 or fewer vertebrae (Ross 1984).

As in all delphinids for which chromosome number is known, the number of chromosomes is $2N = 44$ (Árnason 1974, 1980, Duffield 1977). The G-banded karyotype of *S. frontalis* is not distinguishable from those of *S. clymene* and *Tursiops truncatus* (Árnason 1980). It is similar to that of *S. attenuata*, which is "nearly identical" with that of *S. longirostris* (Worthen 1981). There are slight banding differences between the karyotypes in this group and those of *Lagenorhynchus obliquidens* and *L. albirostris*. The C-banded karyotype of this species exhibits consistent differences from those of *S. longirostris* and *S. attenuata*, which are very similar (Worthen 1981). No clear picture of relationships emerges from these findings.

Ecology—Along the southeastern coast of the United States and in the Gulf of Mexico, the large heavily spotted form of *S. frontalis* inhabits the continental shelf, usually being found inside or near the 100-fathom (183-m) line (within 250–350 km of the coast) but sometimes seasonally coming into very shallow water near the shore, perhaps in pursuit of migratory forage fish (Caldwell and Caldwell 1966, 1973, Schmidly and Shane 1978). It is usually replaced in nearshore shallow waters by *T. truncatus* (Caldwell and Caldwell 1966). The offshore distributions of this form and the other, more oceanic forms in the Caribbean, mid-tropical Atlantic and oceanic western North Atlantic are very poorly known. Recent surveys of small cetaceans in the western North Atlantic, for example, have not distinguished between the two species of spotted dolphins (Erdman *et al.* 1973, Taruski and Winn 1976, Schmidly 1981, Winn 1982, Fritts *et al.* 1983). *S. frontalis* is taken in a subsistence harpoon fishery at St. Vincent in the Lesser Antilles (pers. comm., R. V. Walker). In this area, there is strong morphological convergence with *S. attenuata* (Fig. 18), and the two species may have similar ecologies.

The stomach of a specimen of *S. frontalis* captured off northern Florida contained many small cephalopod beaks, and dolphins of this species have been observed to feed on small clupeoid and carangid fishes and large squid (Caldwell 1955, Caldwell and Caldwell 1966) and to follow trawlers to eat discarded fish (Moore 1953). Of 19 specimens stranded on the U.S. east coast, the stomachs of nine contained only squid remains, six had both fish and squid, and four contained only fish. The otoliths from four of these stomachs were identified to species: a sciaenid *Cynoscion* sp. predominated in one, the sciaenid *Stenotomus chrysops* in two, and a clupeoid *Anchoa* sp. in the fourth; other families represented were Congridae, Gadidae, Trichiuridae and Triglidae (unpublished data, JGM).

Recorded ectoparasites and commensals include the rabbit-eared barnacle *Conchoderma auritum* (van Bree 1971a), the pseudo-stalked barnacle *Xenobalanus globicipitis*, an unidentified cyamid crustacean (Caldwell, Caldwell and Zam 1971) and the remora *Remora* (= *Remilegia*) *australis* (Follett and Dempster 1960). Endoparasites include the trematodes *Campula palliata*, *Pholeter gastrophilus* and *Braunina cordiformis*, and the nematodes *Halocercus delphini* and *Anisakis* sp. (Zam *et al.* 1971).

Life history—Nothing is known of the life history of this species.

Behavior—Pods usually consist of fewer than 50 individuals and most



Figure 18. Adult skulls of *Stenella frontalis* (left, UF SV77-1-SP) and *S. attenuata* (UF SV77-1-SF) from St. Vincent in the Lesser Antilles, demonstrating convergence.

typically of 5 to 15 in coastal waters (Caldwell and Golley 1965, Caldwell and Caldwell 1966, Lowery 1974, Leatherwood *et al.* 1976). Three types of underwater sounds are produced in captivity: whistles, burst-pulses of various kinds, and series of sharp clicks presumed to be for echolocation (Caldwell and Caldwell 1966, 1971). A signature whistle has been identified, but it is less distinctive than in *T. truncatus* (Caldwell *et al.* 1973).

Common name—The established vernacular name "Atlantic spotted dolphin" is suitable for this endemic species.

Specimens included (museum acronyms defined in Appendix 1)—oceanic North Atlantic: Azores, 2 (MNH B2/110, UZMC *Prodelphinus* no. 4); 40°15'N, 29°05'W, 2 (EDM 760, AMNH 239111); 46°20'N, 38°44'W, 1

(EDM 786); 38°40'N, 49°W, 1 (UZMC *Prodelphinus* no. 11); 35°15'N, 74°33'W, 1 (AMNH 239117); 38°05'N, 70°10'W, 1 (MCZ 24800); 38°15'N, 71°17'W, 1 (MCZ 51073); 39°31'N, 69°37'W, 1 (MCZ 51294). Massachusetts: Cape Cod, 1 (USNM 550751, photographs and external measurements only). New York: Amagansett, 1 (USNM 550353). New Jersey: off Cape May, 1 (MCZ 51074); Raritan Bay, 1 (USNM 550099). Maryland: Assateague Island, 2 (USNM 504949 and 550129). Virginia: Lynnhaven Beach, 1 (RAB 030, in possession of R. A. Blaylock); False Cape, 1 (USNM 504758). North Carolina: off Cape Hatteras, 3 (EDM 694 and 695, USNM 22017); Hatteras Island, 1 (USNM 504748); Hatteras, 1 (GWO 020, in possession of Guy W. Oliver); Frisco, 1 (USNM 504736); Buxton, 1 (USNM 550024); Salvo, 1 (USNM 550355); Nags Head, 2 (USNM 504901 and 550101); Bodie Island, 2 (USNM 550098 and 550102); Avon, 1 (USNM 504762); Ocracoke Island, 5 (USNM 504321, 504322, 504862, 504863 and 504876); Topsail Island, 1 (FTI unnumbered, in possession of WFP). South Carolina: off Charleston, 3 (EDM 696 and 697, USNM 253598); Charleston, 1 (MCZ 1182); Bull's Bay, 1 (CM 2555); Hilton Head, 1 (USNM 500858). Georgia: off Georgia, 3 (USNM 261364 and fetus, EDM 844). Atlantic coast of Florida: off St. Augustine, 16 (UF 18727–18739, MLF 294 and stillborn fetus of MLF314, measurements and photographs only of latter two, in possession of DKC); Anastasia Island, 1 (UF 3334); Crescent Beach, 1 (UF 18740); New Smyrna, 1 (UF S-SP-30); Straits of Florida, 2 (EDM 700 and 701); Fort Pierce Inlet, 1 (RSMAS SWF-813); Port Salerno, 1 (RSMAS C-78-3); Miami, 1 (USNM 257833); Hallendale, 1 (RSMAS C-80-5); Upper Matcumbe Key, 1 (RSMAS C-76-12); Content Key, 1 (ANSP 16709). Florida Gulf Coast: St. Petersburg, 2 (UF 18742 and UF R-G-9-SP); off Steinhatchee, 8 (UF 18741 and R-G-2-SP to R-G-8-SP, external measurements and photographs only, in possession of DKC); Eglin Air Force Base, 1 (R-G-10-SP, external measurements and photographs only, in possession of DKC); Destin, 2 (LACM 27057 and 27058); off Pensacola, 1 (USNM 21915); off Boca Grande, 1 (USNM 23414). Louisiana: Johnson's Bayou, Cameron Parish, 1 (MSU 2139). Texas: Port Aransas, 1 (TCWC 1543); off Port Aransas, 3 (USNM 292069-71); Yarbrough Pass, Padre Island, 1 (TCWC 25577). Caribbean: St. Thomas, Virgin Islands, 4 (UF VI-1-SF to VI-4-SF); Puerto Rico, 1 (UZMC *Prodelphinus* no. 10); 17°42'N, 67°22'W, 2 (EDM 808 and AMNH 239116); 19°42'N, 67°50'W, 1 (UZMC *Prodelphinus* no. 14); 14°34'N, 60°03'W, 1 (EDM 803); St. Vincent, Lesser Antilles, 1 (UF SV77-1-SP); 11°02'N, 61°54'W; 2 (AMNH 239112 and 239114); 10°57'N, 61°34'W, 1 (EDM 710); 10°52'N, 66°28'W, 2 (EDM 706 and AMNH 239113); 10°41'N, 66°00'W, 2 (ZMA unnumbered A and B); 9°30'N, 79°00'W, 1 (USNM 254447). Mid-tropical Atlantic: 10°N, 39°W, 1 (UZMC *Prodelphinus* no. 31); St. Helena, 2 (UZMC *Prodelphinus* no. 20 and MNHN A-3031). Africa: 19°03'N, 24°24'W, 1 (UZMC *Prodelphinus* no. 2); Cape Verde, 2 (MNHN A-3034—holotype of *Delphinus frontalis*; MNHN A-3035—holotype of *D. froenatus*); Senegal, 1 (IFAN 76-54); off Vridi, Ivory Coast, 4 (IFAN unnumbered—pregnant female, photographs and measurements only in Cadenat and Lassarat 1959—ZMA 22.964, ZMA 13.148

and ZMA 13.546); Fernando Po, 1 (BMNH [18]62.12.2.6); off Conakry, Guinea, 1 (ZMA 22964); off Pointe Noire, Gabon, 1 (ZMA 15.171). Unknown localities: USNM 3884 (holotype of *Delphinus plagiodon*), BMNH 352.a. (holotype of *D. doris*), BMNH 1948.5.1.1 ("coast of Europe").

Previously unpublished locality records (in addition to those from specimens listed above; sources, when other than authors, listed in ACKNOWLEDGMENTS)—Maine, 1 (48°08'N, 70°39'W—JGM); off New York, 1 (40°37'N, 12°00'W); off Delaware, 2 (38°N, 73°W; 37°N, 74°W); off North Carolina, 4 (35°35'N, 75°20'W; 35°17'N, 74°15'W; 34°49'N, 75°36'W, 34°45'N, 76°45'W); off South Carolina, 1 (approx. 32°50'N, 79°30'W); Bahamas, 1 (approx. 24°N, 74°30'W); Caribbean, 10 (25°11'N, 80°08'W; 24°20'N, 82°48'W; 18°43'N, 74°42'W; approx. 17°30'N, 88°W; 17°03'N, 63°05'W; 14°30'N, 77°10'W; approx. 12°30'N, 70°W; approx. 12°N, 68°W; 11°39'N, 73°50'W; approx. 11°N, 64°W); off Brazil, 1 (approx. 24°S, 46°W); Azores, 2 (approx. 38°N, 28°W).

REDESCRIPTION OF *STENELLA ATTENUATA*

1829. [*Delphinus velox* G. Cuvier, Règne Animal, ed. 2, 1, p. 288.
1840. (or earlier). *Delphinus pseudodelphis* Wiegmann, Schreber's Saeugethiere, pl. 358.
1843. *Delphinus attenuatus* Gray, List mamm. Brit. Mus., p. 105 (*nomen nudum*).
1846. *Steno attenuatus* Gray, Zoology of the voyage of H.M.S. Erebus and Terror, 1 (Mammalia), p. 44, pl. 28.
1884. *Clymenia attenuatus*. Flower, Proc. Zool. Soc. London, 1883, p. 512.
1885. *Clymenia attenuata*. Hector, Trans. N.Z. Inst., 17, p. 211.
1885. *Prodelphinus attenuatus*. Flower, List Cetacea Brit. Mus., p. 30.
1934. *Stenella attenuata*. Iredale and Troughton, Mem. Australian Mus. 6, p. 66.
1975. *Stenella attenuata graffmani* (Lönnerberg) of Perrin, Bull. Scripps. Inst. Oceanogr. 21, p. 125.
1981. *Stenella attenuata attenuata* (Gray) of Hall, Mammals of N.A., p. 882.
1841. *Delphinus malayanus* Schlegel (not Lesson), Abhandl. Gebiete. Zool. u. Vergl. Anat., p. 20 and pl. 2(2).
1923. *Prodelphinus malayanus*. Weber (*sensu* Schlegel 1841), Die Cetaceen der Siboga-Expeditie, p. 8.
1846. *Delphinus brevimanus* Wagner, Schreber's Saeugethiere, 7, pl. 361.
1866. *Steno? brevimanus*. Gray, Cat. seals and whales Brit. Mus., p. 236.
1880. *Prodelphinus brevimanus*. H. Gervais, in van Beneden and Gervais, Ostéographie des Cétacés, p. 605.
1850. *Delphinus? microbrachium* Gray, Cat. Mamm. Brit. Mus., Cetacea, p. 119.

1848. *Delphinus albirostratus* Peale, U.S. Exploring Expedition, Mammalia, p. 34, pl. 7, fig. 2.
1874. *Lagenorhynchus albirostratus*?. Gill, in Scammon, Marine mammals of the north-western coast of North America, p. 293.
1858. *Lagenorhynchus caeruleoalbus*. Cassin, U.S. Exploring Expedition, Mammalogy and Ornithology, p. 31, pl. 6, fig. 2.
1874. *Delphinus ceruleo-albus* of Gill, not Meyen 1833, in Scammon, Marine mammals of the north-western coast of North America, p. 293.
1865. *Steno Capensis* Gray, Proc. Zool. Soc. London, 1865, p. 522.
1884. *[Lymenia] Capensis*. Flower, Proc. Zool. Soc. London, 1883, p. 512.
1898. *Prodelphinus capensis*. Trouessart, Cat. Mamm., p. 1035.
1866. *Clymene punctata* Gray, Proc. Zool. Soc. London, 1865, p. 738.
1866. *Delphinus punctatus*. Gray, Cat. seals and whales Brit. Mus., p. 398.
1871. *Steno consimilis* Malm, Kong. Svensk. Vetensk. Handl., 9, p. 104, pl. 6, figs. 53a, b.
1889. *Prodelphinus alope* Lütken (not Flower 1885), Vid. Selsk. Skrift., Copenhagen, 6, Nat. Mat. 5, 1, p. 43.
1922. *Stenella pseudodelphis* Oliver, Proc. Zool. Soc. London 1922, p. 583.
1934. *Prodelphinus graffmani* Lönnberg, Årk. Zool. Stockholm, 26A, 19, p. 1, pl. 1.
1940. *Stenella graffmani*. Kellogg, Nat. Geogr. Mag., 77, 1, p. 85.

Holotype and type locality—Subadult skull (rostrum still growing), British Museum (Natural History), London (BMNH) no. 347.b., from unknown locality, possibly India (Gray 1843).

Distribution—Worldwide in tropical and some subtropical waters. In Atlantic, broadly sympatric with *S. frontalis* except in oceanic western North Atlantic (Fig. 7) and possibly northern coast of South America. A specimen listed by Lütken (1889; *Prodelphinus* no. 6) as from the Bay of Biscay is actually from off Brazil; the coordinates of latitude and longitude (written on the skull by the collector) are transposed in his paper. There is a single extralimital record from Alaska, with credible locality data; a mummified carcass was found on the beach at Cold Bay on 10 September 1983 (USNM 550771).

Diagnosis—This dolphin is unspotted at birth, with strongly defined cape passing high over the eye, flipper stripe terminating anteriorly at the angle of the gape, and peduncle divided into dark upper and light lower portions (Fig. 1; Perrin 1970, 1972). The typical delphinid eye and blowhole stripes and lip mark are present. The eye stripe is relatively narrow (1–2 cm) and encloses a black eye patch and extension of the eye patch as a black line (a few mm wide) forward to the apex of the melon. The entire eye stripe may be bordered by a narrow light line. The blowhole stripe is relatively narrow and may be composed of sub-elements. The intersection of the anterior end of the flipper stripe and lip mark is demarcated by a narrow light line. The ventral margin of the flipper stripe may be bordered by a narrow light line and subtended by a parallel narrow dark line. A light gray band (4–6 cm) may parallel the ventral margin of the cape. Color at birth is dark gray above and ivory below; the extremities are dark gray. The ventrum darkens to light gray, then dark gray spots appear

ventrally, first in the gular and abdominal regions. Subsequently, light dorsal spots appear. The dark ventral spots increase in number and size until they are largely confluent in adults. The light dorsal spots also increase in size and number and may be confluent in some areas, especially at the ventral margin of the cape over the eye and behind the cape on the upper side of the peduncle. In heavily spotted individuals from some regions (e.g., the Pacific coasts of Mexico and Central America), the ground pattern may be nearly obscured dorsally. Spotting may extend to the dorsal fin and flippers. In adults, several cm of the rostrum and lower jaw may be white. The white may extend posteriorly to edge the entire gape (e.g., Fraser 1950). This feature varies individually and geographically; it is especially prominent in specimens from the western Pacific (Nishiwaki *et al.* 1965).

Minimum and maximum external dimensions and weights for cranially adult specimens from the Atlantic and from all oceans are presented in Table 3. Maximum recorded length for males is 257 cm and for females 240 cm (both from the eastern tropical Pacific). The smallest known cranially adult specimens (a male of 166 cm and female of 163 cm) were also from the eastern tropical Pacific. Adult length in the species thus varies about 1 m (roughly 50 percent of midpoint length of about 2 m).

A typical skull from the western North Atlantic is illustrated in Figure 11. Ranges of skull measurements for cranially adult specimens and postcranial measurements for physically mature specimens are in Table 4 for the Atlantic and for all oceans. Development and variation of the complete skeleton were described and illustrated by Perrin (1975). The largest known skull is of the above-mentioned 257-cm male (119 kg) from the Gulf of Panama in the eastern Pacific (USNM 261432). Ranges are not presented separately for males and females in Table 4 because the substantial geographic variation in this species (discussed below) could be expected to obscure sexual dimorphism. Slight sexual dimorphism does exist in several skull dimensions and has been described for samples from the eastern Pacific (Table 9; also Perrin 1975, Schnell *et al.* 1985). Females tend to have a longer rostrum and males a larger braincase, but there is very great overlap in all characters.

Rostral tooth counts range from 35 to 48 and mandibular counts from 34 to 47 and average about 40 in each jaw (Table 5). The number of vertebrae ranges from 74 to 84 (but note that the specimen with the isolated value of 74—UZMC *Prodelphinus* no. 6—may represent a case in which one or more vertebrae were lost during preparation of the specimen; the specimen with 76 vertebrae is also in the Copenhagen Museum—*Prodelphinus* no. 15). The typical vertebral formula is C7, T16, L20, Ca37 = 80.

Geographic variation—The species varies geographically in coloration, body size and cranial and postcranial measurements. This has been demonstrated based on large series of specimens from the eastern tropical Pacific (Perrin 1975, Perrin *et al.* 1979, Douglas *et al.* 1984, Perrin *et al.* 1985, Schnell *et al.* 1986). Material from other parts of the Pacific, from the Indian Ocean and from the Atlantic is still too limited to support more than very tentative conclusions concerning geographic variation involving those areas.

As noted above, degree of spotting varies geographically in the eastern

Table 9. Skull measurements (mm) exhibiting sexual dimorphism in *Stenella attenuata* (from Schnell *et al.* 1985; unweighted means of mixed sample of 543 specimens drawn from two or more populations in eastern Pacific).

Measurement	Mean		P ^a
	Male	Female	
Length of rostrum	239.4	242.5	***
Width of rostrum at base	85.2	83.8	***
Width of rostrum at ¼ length	59.6	57.9	***
Width of rostrum at ½ length	44.4	42.9	***
Width of premaxillaries at ½ length	24.1	22.8	***
Width of rostrum at ¾ length	31.9	30.1	***
Rostrum tip to internal nares	281.6	284.3	**
Greatest preorbital width	152.3	149.5	***
Greatest postorbital width	170.5	167.9	***
Zygomatic width	170.5	167.3	***
Greatest width of pmx's	67.5	66.9	**
Parietal width	141.3	138.0	***
Height of braincase	99.2	96.9	***
Int. length of braincase	120.1	117.9	***
Greatest width of left pmx	26.6	26.1	***
Length of temporal fossa	68.8	67.1	***
Width of temporal fossa	52.9	51.1	***
Length of preorbital process	38.3	37.6	**
Width of int. nares	48.0	47.2	***
Length of upper toothrow	204.7	207.4	***
Length of lower toothrow	199.0	201.8	***
Length of ramus	339.0	342.2	**
Diameter of tooth (at mid-length of lower row, transverse at alveolus)	3.82	3.70	***

^a **, $P < 0.01$; ***, $P < 0.001$.

Pacific. Dolphins close to the coast are on the average more heavily spotted than those that are more offshore (Perrin 1975). Specimens from the western Pacific (Nishiwaki *et al.* 1965), the southern Indian Ocean (Ross 1984), Africa (Fraser 1950) and the mid-tropical Atlantic (field observations by WFP at St. Helena) are spotted to about the same extent as those in the offshore eastern Pacific, although in some areas (*e.g.*, Hawaii and St. Helena) dorsal spotting in some adults is so weakly developed as to give the animal an unspotted appearance when seen at a distance.

Body size also varies geographically (Table 10). Coastal spotted dolphins from the eastern tropical Pacific are the largest (males and females averaging 223 and 207 cm, respectively), followed closely by those from the coastal western North Atlantic and Gulf of Mexico. Of those regions for which adequate samples exist, the oceanic eastern tropical Pacific is inhabited by the smallest animals; males average 200 cm ($n = 1,280$) and females 187 cm ($n = 3,890$). Only single lengths are available for the Caribbean (a 191-cm female; SV77-1-SF) and Africa (a 200-cm male; the BMNH *Atlantide* specimen), values that fall within the ranges for all the large samples from other regions.

Table 10. Geographic variation in body length (cm) in *Stenella attenuata* (sample size in parentheses).

Eastern Pacific ^{a,b}										Coastal eastern N. Atlantic & Gulf of Mexico
Oceanic (offshore)							S.W. Indian Ocean ^c	Western N. Pacific ^c		
Northern				Southern						
	Coastal	W. of 120°W	E. of 120°W							
Mean	M	223.2 (47)	198.6 (200)	200.1 (994)	196.6 (86)	204-207 (80)	—	215.8 (5)		
	F	206.5 (87)	186.6 (499)	187.8 (3,077)	185.3 (314)	192-195 (251)	—	188.3 (3)		
Range	M	197-246 (47)	177-228 (200)	166-240 (994)	175-220 (86)	max 234 (>300)	216-220 (2)	193-231 (5)		
	F	179-227 (87)	165-215 (499)	163-215 (3,077)	168-206 (314)	173-220 (>344)	215 (1)	186-194 (3)		
SD	M	11.73 (47)	9.10 (200)	9.46 (994)	7.52 (86)	—	—	—		
	F	10.47 (87)	7.34 (499)	7.28 (3,077)	7.12 (314)	—	—	—		

Length also varies geographically within the oceanic eastern Pacific; samples from different latitudinal/longitudinal strata differ by as much as 3 cm in average body length (Table 10). It is not yet known if this reflects the existence of only clinal variation or the existence of more than one breeding population.

Variation in skull size and size of the postcranial skeleton in the eastern Pacific parallels that in body size (Perrin 1975, Douglas *et al.* 1984); the coastal form has a much larger skull and larger postcranial bones than does the oceanic form (Tables 11 and 12). The temporal fossa is especially large; the means for the two measurements of this feature (as well as height of ramus and tooth diameter) in the coastal series lie outside the ranges for the measurements for all 55 specimens from other waters in the Atlantic, Pacific and Indian Oceans. This is also true for the height of the mandibular ramus. The largest skull known for the species (CB length 460 mm; illustrated in Perrin 1975) is in this series.

Geographical variation in the cranium also exists within the oceanic eastern tropical Pacific (Perrin *et al.* 1979, Schnell *et al.* 1986); skulls of dolphins from north of the equator differ from those from south of the equator in being on the average larger and having proportionately larger temporal fossae. Specimens from the far western portion of the range in the eastern Pacific show affinities with those from south of the equator in the east and with specimens from Hawaii. As noted above, it is not yet known if this variation is wholly clinal or if it reflects the existence of two or more breeding populations. Schnell *et al.* (1986) found correlations between the north/south variation and several environmental variables, including annual solar insolation and sea-surface temperature.

The specimens in the series from the oceanic eastern Pacific and from St. Helena in the Atlantic are on the average smaller than those from other areas, and the specimens in the series from the coastal western North Atlantic, Hawaii, the western Pacific and the Indian Ocean are intermediate.

Virtually nothing is known about the species in the eastern North Atlantic and in the Southern Hemisphere aside from St. Helena. The five specimens from Africa and South America are listed individually in Table 11 because of their broad provenance and diversity. The skull from the Gulf of Guinea is the shortest known for the species from the Atlantic. As noted by Best (1969) and Ross (1984), this is because of its very short rostrum (illustrated in Fraser 1950); in other features it does not differ materially from other Atlantic specimens. The skulls from Cape Verde and Argentina are small and similar to those from St. Helena and the oceanic eastern Pacific, but the two skulls from Brazil are the largest known for the species from the Atlantic. It is evident that much more material must be in hand before geographic variation in the Atlantic can be adequately described. The same is true for the Indian Ocean (as noted by Ross 1984) and the central, southern and western Pacific.

The specimen from Alaska is problematical. The rostrum is extremely long, but in other dimensions it conforms well with the oceanic form in the eastern tropical Pacific.

Stenella attenuata also varies geographically in meristic characters. Douglas

et al. (1984) detected a mean difference of approximately one tooth per row between the coastal and oceanic forms in the eastern Pacific (40.4/39.4 and 41.3/40.2, respectively). Only the series of specimens from St. Helena is large enough to allow comparison with the eastern Pacific series. Average of highest rostral and mandibular counts in that series are 41.0 and 39.9, respectively ($n = 42$ and 43 ; $SD = 2.12$ and 2.19), closest to the eastern Pacific coastal form (when the upwardly biasing effect of using highest count rather than average of left and right counts is considered). Tooth counts for the Atlantic specimens overall are approximately $\frac{1}{2}$ tooth lower than for all specimens pooled (Table 5).

Coastal spotted dolphins in the eastern Pacific have on the average about 78 vertebrae, as opposed to about 80 in the oceanic form (Fig. 19). The series from other regions are too small to allow comparisons (Table 5).

Comparisons—See redescription of *S. frontalis* above for comparisons with that species and with *S. longirostris*, *S. clymene*, *S. coeruleoalba*, *Delphinus delphis*, *Lagenodelphis hosei* and *Tursiops truncatus*.

Ecology—The species occurs both in coastal waters and in the open ocean. In the eastern tropical Pacific it commonly associates with schools of yellowfin tuna (*Thunnus albacares*) and may be found together with tuna, spinner dolphins (*S. longirostris*) and large numbers of sea birds. This multispecies aggregation is correlated in distribution with certain oceanographic variables, including depth and steepness of the thermocline and sea-surface temperature, and may constitute a symbiotic foraging association involving two or more of the species (Au and Perryman 1985). The existence of greater morphological differences between *S. attenuata* and *S. longirostris* in this region than exist between them in other places where they do not school and forage together (*e.g.*, Hawaii, just to the west) may indicate that ecological character displacement has occurred (Perrin 1985b). Large numbers of spotted dolphins are killed incidentally by tuna seining operations in the eastern tropical Pacific and at least two populations there have declined in size (Smith 1983).

Recorded stomach contents include a large number of small epipelagic and mesopelagic fishes and squids and unidentified nemertean worms and crab larvae (Fitch and Brownell 1968, Perrin *et al.* 1973, Shomura and Hida 1965, Ross 1984). Fish families represented are Exocoetidae, Scombridae, Myctophidae, Gonostomatidae, Bregmacerotidae, Gempylidae, Paralepididae, Alepisauridae, Bramidae, Bathylagidae, Trichiuridae, Congridae, Scopelosauridae, Opisthoproctidae, Evermannellidae, Balistidae, Melamphaidae and Stromateidae. Cephalopod remains were of the families Onychoteuthidae, Ommastrephidae, Enoploteuthidae, Histioteuthidae, Chiroteuthidae, Cranchiidae, Lycoteuthidae and Octopoteuthidae. Lactating females may feed more heavily on epipelagic fish than do pregnant females (Bernard and Hohn 1985).

Ectoparasites and commensals include a cyamid amphipod *Syncyamus* sp. (Leung 1970) and the barnacles *Conchoderma auritum* (Perrin 1969) and *Xenobalanus globicipitis* (Ross 1984). Endoparasites include the cestodes *Tetrabothrium forsteri*, *Strobilocephalus triangularis*, *Phyllobothrium delphini* and *Monorygma delphini*, the trematodes *Nasitrema globicephalae*, *N. stenosoma*,

Table 11. Statistics of cranial measurements (mm) for geographical series of *Stenella attenuata* (sample size in parentheses).

Atlantic													
	Africa ^b						S. America						
	Cape Verde		Gulf of Guinea		Fer- nando de No- ronha	Coast of Brazil	Uru- guay	MACNBA	23-46				
	ZMA-IFAN		BMNW									CMNH	MCNRS ^c
	no.	32	no.	32									
	Coastal N.W. Atlantic & Gulf of Mexico		St. Helena (11) ^a										
	Mean	Range	Mean	Range									
Condylobasal length	415.3	403-432 (10)	401.1	387-423	388	369	437	440	389				
Length of rostrum	253.3	243-271 (10)	240.0	231-260	232	208	268	270	221				
Width of rostrum at base	88.1	78-93 (10)	86.2	82-94	84	85	95	90	92				
Width of rostrum at ¾ length	30.6	27-33 (10)	27.6	25-32	28	31	36	46	31				
Zygomatic width	175.1	171-182 (10)	171.2	163-178	169	171	182	185	177				
Greatest width of pmx's	70.4	65-73 (10)	67.7	65-70	66	69	75	73	69				
Parietal width	140.0	131-146 (10)	138.6	131-145	138	146	150	151	142				
Length of temporal fossa	68.0	63-73 (10)	65.4	63-70	58	66	64	65	61				
Height of temporal fossa	52.1	45-55 (10)	50.0	43-56	45	59	56	56	45				
Length of upper toothrow	216.2	200-235 (10)	205.0	194-224	196	175	228	224	196				
Length of ramus	356.5	345-375 (9)	341.1	328-362	331	312	370	—	343				
Height of ramus	58.0	55-61 (9)	57.9	53-62	57	61	59	—	57				
Diameter of tooth (at midlength of lower row, transverse at alveolus)	3.37	3.0-3.5 (6)	3.50	3.3-3.7	—	—	4.1	—	—				

Table 11. Continued.

	Pacific Ocean						Alaska (1)	Indian Ocean ^g	
	Eastern Pacific ^d		Hawaii ^e		Western Pacific ^f				
	Coastal (31)	Oceanic (575)	Mean	Range	Mean	Range			
Condylobasal length	436.7	396.1	413.6	395-440 (12)	412.4	400-433 (12)	435	410.2	345-423 (6)
Length of rostrum	262.3	237.1	250.8	240-269 (12)	249.2	243-258 (12)	270	247.8	233-261 (6)
Width of rostrum at base	90.5	83.0	89.2	86-94 (13)	87.7	78-95 (12)	85	87.6	87-89 (5)
Width of rostrum at ¼ length	35.6	29.6	31.8	28-35 (12)	30.9	28-34 (12)	30	31.2	29-35 (5)
Zygomatic width	180.9	165.3	172.2	164-181 (13)	168.7	159-183 (12)	179	174.7	166-183 (6)
Greatest width of pmx's	72.3	65.8	68.9	65-71 (13)	68.3	61-76 (12)	69	67.8	65-70 (6)
Parietal width	147.8	138.3	141.0	135-150 (13)	140.7	130-152 (12)	144	135.0	131-138 (6)
Length of temporal fossa	81.1	65.8	62.0	57-70 (13)	64.8	61-70 (10)	66	66.8	62-72 (6)
Height of temporal fossa	61.0	50.7	50.2	42-56 (13)	51.8	47-55 (10)	51	50.8	46-56 (6)
Length of upper toothrow	225.6	202.9	215.9	200-232 (12)	214.5	204-232 (13)	226	211.0	199-223 (6)
Length of ramus	370.6	335.5	351.4	339-379 (12)	353.2	340-374 (13)	369	346.7	334-355 (6)
Height of ramus	66.0	57.2	57.5	53-61 (13)	58.4	55-61 (12)	61	57.7	56-61 (6)
Diameter of tooth (at midlength of lower row, transverse at alveolus)	4.73	3.51	—	—	—	—	3.4	—	3.8 (1)

^a All of unknown sex.^b ZMA-IFAN no. 32 is of unknown sex; BMNH "Atlantide" is a male.^c From Pinedo and Castello (1980).^d From Douglas *et al.* (1984); averages of pooled males and females adjusted for sex to "zwittier" values.^e From Perrin (1975).^f Eight specimens examined, three from Nishiwaki *et al.* (1965), two from Zhou *et al.* (1980).^g Three specimens examined, two from Ross (1984), one from Best (1969).

Table 12. Statistics of postcranial measurements (mm) for geographical series of *Stenella attenuata* (sample size in parentheses).

	Atlantic					Pacific				Hawaii		Indian Ocean	
	Coastal N.W. Atlantic & Gulf of Mexico (5)			Africa (1)		BMNH "Atlantic-tide"	Eastern Pacific coastal		Eastern Pacific oceanic ^a		USNM	UBC	SAM
	Mean	Range	Range	Mean	Range		Mean	Range					
Atlas: width	77.4	73-83		80	86.8	82-90 (5)	77.8	73-84 (16)	90	82	84	—	—
First thor. vert. width	75.4	72-79		74	79.8	77-82 (5)	71.8	63-80 (16)	84	86	—	—	—
First lumb. vert. width	189.6	175-202		179	193.5	180-207 (5)	174.8	165-188 (15)	—	200	—	—	—
Length of longest vert. rib	261.8	234-286		256	292.0	281-313 (4)	248.9	232-263 (16)	265	270	—	—	—
Scapula: height	119.2	112-127		105	130.0	126-135 (5)	108.2	101-123 (16)	124	117	103	—	—
Humerus: length	52.0	50-56		50	57.0	53-62 (5)	48.1	43-53 (16)	51	50	51	51	51

^a From Perrin (1975).

^b From Best (1969).

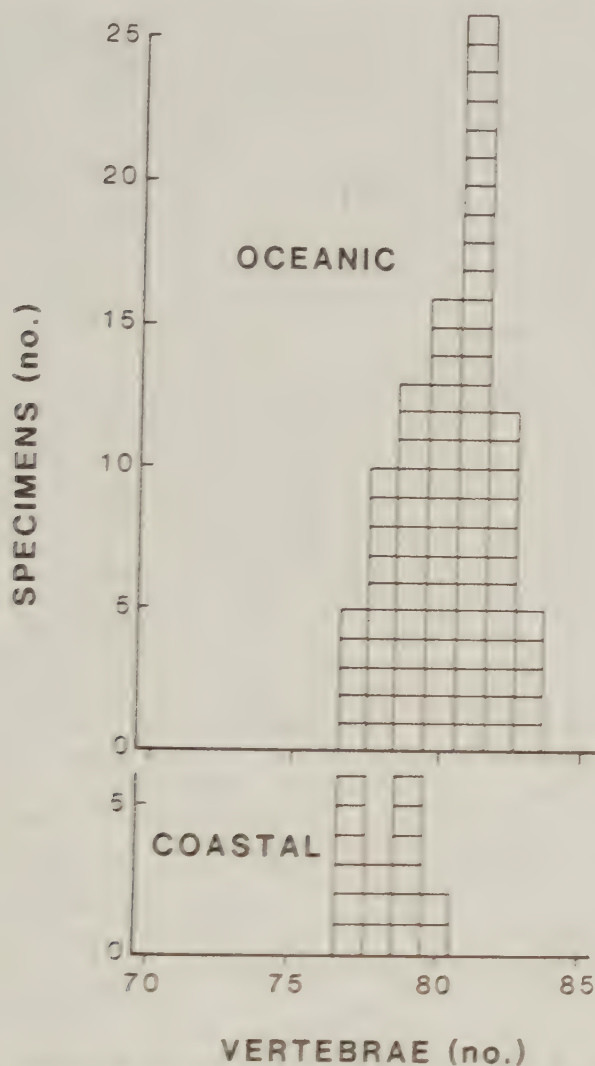


Figure 19. Number of vertebrae in coastal and oceanic specimens of *Stenella attenuata* in the eastern Pacific.

Campanula ruberrima, *Orthoplutonium ? elongata* and *Zalophorema pacificum*; the nematodes *Acanthi simplex*, *A. rigida*, *A. alexandri*, *Mamigonema stenellae*, *Hawkeria dispersa* and *Crauslandia* sp. and the acanthocephalans *Bolbosoma novaeboracae* and *B. salweenae* (Nelson *et al.* 1970, Daley and Perrin 1973, Zhou *et al.* 1980, Daley and Otto 1982, Ross 1984).

Predators include one or more of the carcharoid sharks, the cookie-cutter shark (*Isurus paucus*) and the killer whale (*Orcinus orca*); in addition they

may include other sharks, the false killer whale (*Pseudorca crassidens*), the pygmy killer whale (*Feresa attenuata*) and the short-finned pilot whale (*Globicephala macrorhynchus*) (Leatherwood *et al.* 1973, Perryman and Foster 1980, WFP, unpub. data).

Behavior—Pods range in size from a few dolphins to several thousand (Scott *et al.* 1985). For oceanic populations, home range may be several hundred kilometers or more in diameter, within which seasonal migrations occur (Perrin *et al.* 1979). The species migrates into Japanese waters seasonally, following the northern edge of the warm Kuroshio Current (Miyazaki *et al.* 1974). This dolphin often rides the bow waves of ships (Leatherwood *et al.* 1982). Two trained specimens reached a top speed of 11.03 m/sec (21.4 knots) in 2.0 seconds (Lang and Pryor 1966).

Life history—Average age at sexual maturation in males is 14.7 yr (Hohn *et al.* 1985). Females mature on the average at 10–12 yr (Myrick *et al.* 1986); the range is 10 to 17 yr. Maximum longevity in both sexes may exceed 45 yr (Kasuya 1985). Aged females may become postreproductive (Perrin *et al.* 1976, Myrick *et al.* 1986). Average calving interval in the eastern Pacific is 2 to 3 yr and in the western Pacific 4 to 6 yr, the difference possibly related to differential status of the populations (Kasuya 1985, Myrick *et al.* 1986).

Common name—We propose that the vernacular name "pantropical spotted dolphin" be used for this species.

Specimens included (museum acronyms defined in Appendix 1)—Massachusetts: Revere, 2 (USNM 550016–17). Rhode Island: Charleston, 1 (USNM 550356). North Carolina: Carolina Beach, 1 (NCSM 2564). Atlantic Coast of Florida: Fernandina Beach, 1 (UF R-2-SF); New Smyrna Beach, 1 (UF 18984); Sebastian [?], 1 (MCZ 20584); Port Canaveral, 1 (RSMAS SWF-829); Fort Lauderdale, 1 (RSMAS C-77-9); near Soldier Key (near Miami), 1 (UF R-1-SF); Coconut Grove, 1 (USNM 218344). Gulf Coast of Florida: Pensacola, 2 (USNM 550374; UF R-G-2-SF); Panama City, 4 (external photos only, USNM MME00174); Big Pass (near Sarasota), 1 (UF R-G-1-SF). Caribbean: St. Vincent, 2 (UF SV-77-1-SF and SV-1-SF). Brazil: Isla Fernando de Noronha, 1 (CMNH 2524); Rio Grande, 1 (MCNRS 026—not examined, data from Pinedo and Costello 1980). Uruguay: 1 (MACNBA 23-46—not examined, data from Brownell and Praderi 1976). Mid-tropical Atlantic: 11°N, 47°W, 1 (UZMC *Prodelphinus* no. 6); 9°N, 33–34°W, 1 (UZMC *Prodelphinus* no. 3); 6°46'N, 24°35'W, 1 (AMNH 39092); 2°44'N, 29°W, 1 (UZMC *Prodelphinus* no. 8). St. Helena: 44 (USNM 347651; BMNH 1946.9.10.4, 1956.11.2.1–6, 1957.5.9.1–8, 1958.5.27.1–3, 1959.2.23.1–8, 1959.12.31.1–11, 1960.6.24.1–5, 1961.11.24.1). Africa: Cape Verde, 2 (ZMA 22.962; PML unnumbered—holotype of *Clymene punctata*, not examined, data from Gray 1966 and True 1889); Gabon, 1 (BMNH Atlantide specimen). "Southeast Atlantic": 1 (MCZ 7942). "South Atlantic": 1 (MCZ 1187). "Mid Atlantic": 1 (BMNH 1878.2.11.1). "Atlantic Ocean": 2, (UZMC *Prodelphinus* no. 21, 24). Red Sea: Koseir, 2 (ZMB 31975, LIZ 6886). Persian Gulf: Siham, 1 (BMNH 73.1749). Indian Ocean: Seychelles, 2 (BMNH 347.e, f); Amirante Islands, 2 (USNM 36049–50); Alphonse Island, 1 (USNM 36131); Providence Island, 1 (USNM 36051); Île d'Anjouan, 1 (USNM

36048); Madagascar, 2 (MNHN 1928-162, A-3037); 28°20'S, 60°E, 1 (UZMC *Prodelphinus* no. 15); South Africa, 5 (BMNH 1878.2.11.1, SAM 35515—not examined, data from Best 1969—, PEM 1520/84, 1517/68, 1520/85—not examined, data from Ross 1984); "Indian Ocean," 2 (RMNH cat. b no. 19, MNHN A-3029); Djibouti, 1 (MNHN 1981-185—not examined, data from Robineau and Rose 1984). Western Pacific: Indonesia, 4 (MNHN A-3028, 1882-113, 1882-305; USNM 49873); China, 2 (NJNU 7803-4—not examined, data from Zhou *et al.* 1980); Japan, 9 (BMNH 1966.6.14.1, TKO 102-4 and 4 unnumbered—not examined, data from Nishiwaki *et al.* 1965, unnumbered specimen in Ogawa 1936—not examined); Solomon Islands, 12 (BMNH 1966.11.18.2, 3, 5, 8; WHD 278, 289, 440, 444, 451, 452, 456, 459). Hawaii: 16 (15 listed in Perrin 1975, MNHN 1874-642). Alaska: 1 (USNM 550771). Eastern tropical Pacific (in addition to 132 listed in Perrin 1975 and 19 in Perrin *et al.* 1979): 12 km north of Mazatlan, Mexico, 1 (ZMA 16.204); 20°26'N, 106°32'W, 9 (SDMNH 23552-54, 235645-6; SWFC DJT 39, 40, 42, 46); 18°18'N, 103°50'W, 1 (SWFC TCB 36); 16°16'N, 98°52'W, 1 (UZMC *Galathea* CN 1); 11°44'N, 132°26'W (NMNS JOH 14); 9°39'N, 106°17'W, 2 (MNHN 1982-97, 99); 9°27'N, 109°44'W, 1 (NSM BGT 18); 9°00'N, 101°57'W, 4 (MNHN 1982-93, 94, 95, 96); 8°57'N, 102°05'W, 7 (MNHN 1982-84, 87, 88, 89, 90, 92, 117); 8°42'N, 105°20'W, 1 (SWFC AXB 23); 8°29'N, 140°48'W, 1 (LACM 72313); 8°18'N, 138°10'W, 1 (LACM 72312); 8°17'N, 138°33'W, 1 (LACM 72310); 8°16'N, 140°46'W, 1 (SWFC JWG 57); 8°15'N, 132°20'W, 1 (LACM 72314); 8°13'N, 98°32'W, 1 (TCWC TAL 4); 8°13'N, 135°20'W, 1 (NMNS VFC 32); 7°30'N, 130°58'W, 1 (LACM 72315); 7°18'N, 132°57'W, 1 (LACM 72316); 5°54'N, 129°40'W, 1 (LACM 72322); 4°55'N, 107°45'W, 1 (NMNS RMB 24); 4°40'N, 105°15'W, 1 (NMNS RMB 47); 2°55'N, 119°20'W, 1 (NMNS DAA 169); 2°53'S, 98°45'W, 2 (SWFC GCF 7, 10); 6°02'S, 85°46'W, 2 (NMNS SRM 45, 46); 8°48'S, 89°21'W, 1 (SWFC SFG 3); 8°53'S, 90°47'W, 6 (SDMNH 23571 and 23749, WSL 13, 14, 15, 17; SWFC WSL 18); 9°03'S, 84°28'W, 1 (SWFC SRM-A); 9°08'S, 90°34'W, 1 (SDMNH WSL 5); 9°12'S, 91°33'W, 1 (SDMNH 23751); 12°12'S, 83°17'W, 2 (LACM WFP 681, 682). Unknown localities: 2 (BMNH 347.B., ZMUB 12009—only photographs examined, other data from True 1889).

Previously unpublished locality records (in addition to those from specimens listed above; sources, when other than authors, listed in ACKNOWLEDGMENTS)—Florida, 1 (26°55'N, 80°05'W—JGM); Gulf of Mexico, 1 (23°00'N, 84°28'W); Caribbean, 8 (20°14'N, 84°35'W; 20°06'N, 84°29'W; 18°52'N, 74°50'W; 18°43'N, 74°42'W; 14°11'N, 61°W; 13°12'N, 61°27'W; near Grenada, 2 sightings); St. Helena (multiple sightings—WFP).

ACKNOWLEDGMENTS

The late Francis C. Fraser of the British Museum gave us his files of notes, measurements and photographs relating to his research on the systematics of *Stenella* upon his retirement in 1973; the work reported here owes much to his material help and encour-

agement. William E. Schevill of the Museum of Comparative Zoology, Daniel K. Odell of the Rosenstiel School of Marine and Atmospheric Science (RSMAS) at the University of Miami, the late Raymond M. Gilmore of the San Diego Museum of Natural History and Robert V. Walker of the University of Washington also gave us free access to unpublished data and specimens garnered at great expanse of time, effort and money. Many others gave us access to specimens in their charge and otherwise assisted us in our museum work: S. Anderson, R. G. Van Gelder and D. H. Russel of the American Museum; A. E. Sanders of the Charleston Museum; D. Lee of the North Carolina State Museum; S. R. Humphrey and L. Wilkins of the Florida State Museum; D. R. Patten and J. E. Heyning of the Los Angeles County Museum; A. Rea and S. Bond of the San Diego Museum of Natural History; M. C. Sheldrick and D. Mills of the British Museum; C. Camillo of the Cleveland Museum; M. E. Rutzmoser of the Museum of Comparative Zoology; M. S. Hafner of Louisiana State University; F. W. Braestrup, P. Valentin-Jensen and H. J. Baagoe of the Zoological Museum in Copenhagen; E. Zubtsova and the late A. S. Sokolov of the Zoological Institute in Leningrad; D. J. Schmidly and S. H. Shane of Texas A & M University; C. W. Potter of the U.S. National Museum; D. Robineau of the Paris Museum; R. D. Estes of the Academy of Natural Sciences of Philadelphia; C. Smeenk of the State Museum in Leiden; Dr. J. Lepiskaar of the Goteborg Museum; R. A. Angermann of the Zoological Museum in Berlin; and the late M. Nishiwaki of the Ocean Science Institute in Tokyo. G. W. Oliver and R. A. Blaylock gave us access to privately owned specimens. The following gave us unpublished locality records: F. Cervigon, R. Duguy, S. Earle, W. E. Evans, H. Hauser, A. R. Martin, D. A. McBrearty, K. E. Moore, R. L. Pitman, C. M. Poppe, H. W. Pratt, D. Robineau, L. Rosen, S. S. Sadove, G. di Sciara, H. E. Winn, L. A. Zavala-Camin and J. A. Zwack. The late J. E. Fitch identified otoliths from stomach contents of *S. frontalis*. V. M. Kozicki and others at the Arctic Biological Station aided us in the field and with laboratory and museum work. D. Robineau, R. L. Brownell, Jr., J. Barlow, J. E. Heyning, D. W. Rice, G. D. Schnell, L. G. Barnes, Zhou Kaiya and I. Barrett reviewed the manuscript. We thank all of these people and others we may have missed for their help in a project that was made possible only by very wide collaboration and pooling of information.

LITERATURE CITED

- ALLEN, G. M. 1925. The bridled dolphin (*Prodelphinus froenatus*) on the Florida coast. *Journal of Mammalogy* 6:59.
- ALLEN, G. M. 1931. Ocean dolphins. *Bulletin of the Boston Society of Natural History* 61:3-7.
- ÁRNASON, Ú. 1974. Comparative chromosomes studies in Cetacea. *Hereditas* 77:1-36.
- ÁRNASON, Ú. 1980. C- and G-banded karyotypes of three delphinids: *Stenella clymene*, *Lagenorhynchus albirostris* and *Phocoena phocoena*. *Hereditas* 92:179-187.
- AU, D. W. K., AND W. L. PERRYMAN. 1985. Dolphin habitats in the eastern tropical Pacific. *Fishery Bulletin* 88:623-643.
- BERNARD, H. J., AND A. A. HOHN. 1985. Food habits of pregnant and lactating spotted dolphins in the eastern tropical Pacific [Abstract]. Abstracts Sixth Biennial Conference on the Biology of Marine Mammals, Vancouver, British Columbia, November 22-26, 1985, unpaginated.
- BEST, P. B. 1969. A dolphin (*Stenella attenuata*) from Durban, South Africa. *Annals of the South African Museum* 52:121-135 + pl. 11-17.
- BEST, R. C., J. M. DA ROCHA AND V. M. F. DA SILVA. 1985. Registro de pequenos cetáceos na costa nordeste Brasileira. [Proceedings of] Primera Reunion de Trabajo de Expertos en Mamíferos Acuáticos de America del Sud, Buenos Aires, 25-29 June 1984.
- BREE, P. J. H. VAN. 1971a. The rabbit-eared barnacle, *Conchoderma auritum*, on the

- teeth of the dolphin *Stenella frontalis*. Zeitschrift fuer Saeugetierkunde 36:316-317.
- BREE, P. J. H. VAN. 1971b. On the taxonomic status of *Delphinus pernettensis* de Blainville, 1817. Beaufortia 244:21-25.
- BREE, P. J. H. VAN. 1975. Preliminary list of the cetaceans of the southern Caribbean. Studies on the Fauna of Curaçao and other Caribbean Islands 48:79-87.
- BRIMLEY, C. S. 1946. The mammals of North Carolina. Installment No. 17. Carolina tips. Carolina Biological Supply Company, Elon College, North Carolina. Irregular pagination.
- BROWNELL, R. L., JR., AND R. PRADERI. 1976. Records of the delphinid genus *Stenella* in western South Atlantic waters. Scientific Reports of the Whales Research Institute. Tokyo 28:129-135 + pl. 1.
- CADENAT, J. 1956. A propos de cachalot. Notes Africaines 71:82-92.
- CADENAT, J. 1959. Rapport sur les petits Cétacés ouest-africains. Résultats des recherches entreprises sur ces animaux jusqu'au mois de mars 1959. Bulletin de l'Institut Français d'Afrique Noire 21, Ser. A:1367-1409 + pl. 1-31.
- CADENAT, J., AND A. LASSARAT. 1959. Notes sur les delphinidés ouest-africains. IV. Sur un *Prodelphinus* indéterminé de Côte d'Ivoire. Bulletin de l'Institut Français d'Afrique Noire 21, Ser. A:777-786.
- CALDWELL, D. K. 1955. Notes on the spotted dolphin, *Stenella plagiodon*, and the first record of the common dolphin, *Delphinus delphis*, in the Gulf of Mexico. Journal of Mammalogy 36:467-470.
- CALDWELL, D. K. 1960. Notes on the spotted dolphin in the Gulf of Mexico. Journal of Mammalogy 41:134-136.
- CALDWELL, D. K., AND M. C. CALDWELL. 1966. Observations on the distribution, coloration, behavior and audible sound production of the spotted dolphin, *Stenella plagiodon* (Cope). Los Angeles County Museum Contributions in Science 104. 28 pp.
- CALDWELL, D. K., AND M. C. CALDWELL. 1971. Underwater pulsed sounds produced by captive spotted dolphins, *Stenella plagiodon*. Cetology 1. 7 pp.
- CALDWELL, D. K., AND M. C. CALDWELL. 1973. Marine mammals of the eastern Gulf of Mexico. Pages III-1-1-16 in J. I. Jones, R. E. Ring, M. O. Rinkel and R. E. Smith, eds. A summary of knowledge of the eastern Gulf of Mexico. State University System of Florida Institute of Oceanography, St. Petersburg, FL.
- CALDWELL, D. K., M. C. CALDWELL, W. F. RATHJEN AND J. R. SULLIVAN. 1971. Cetaceans from the Lesser Antillean Island of St. Vincent. Fishery Bulletin 69:303-312.
- CALDWELL, D. K., M. C. CALDWELL AND S. G. ZAM. 1971. A preliminary report on some ectoparasites and nasal-sac parasites from small odontocete cetaceans from Florida and Georgia. Pages 1-7 in S. G. Zam, D. K. Caldwell and M. C. Caldwell, eds. Studies on cetacean parasites. Marineland Research Laboratory Technical Report 5, submitted to the Office of Naval Research under Contract no. N00014-70-C-0178.
- CALDWELL, D. K., AND F. B. GOLLEY. 1965. Marine mammals from the coast of Georgia to Cape Hatteras. Journal of the Elisha Mitchell Scientific Society 81: 24-32.
- CALDWELL, M. C., D. K. CALDWELL AND J. F. MILLER. 1973. Statistical evidence for individual signature whistles in the spotted dolphin, *Stenella plagiodon*. Cetology 16. 21 pp.
- CASSIN, J. 1858. United States Exploring Expedition. Mammalogy and Ornithology. J. B. Lippincott, Philadelphia, PA. 466 pp. + atlas.
- COPE, E. D. 1865. A contribution to the knowledge of the Delphinidae. Proceedings of the Academy of Natural Sciences of Philadelphia 1865:198-204.
- COPE, E. D. 1866. Third contribution to the history of the Balaenidae and Delphinidae. Proceedings of the Academy of Natural Sciences of Philadelphia 1866:293-299.

- CUNÍ, L. A. 1918. Contribución al estudio de mamíferos acuáticos observados en las costas de Cuba. Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey" 3:83-123.
- CUVIER, F. 1829. Cétacés. In E. Geoffroy Saint-Hilaire and F. Cuvier, eds. Histoire naturelle des Mammifères, Vol. 3, Sections 57-59. A. Belin, Paris.
- CUVIER, F. 1836. De l'Histoire naturelle des Cétacés, ou Recueil et examen des Faits dont se compose l'Histoire de ces Animaux. Librairie Encyclopedique de Roret, Paris. iv + iii + 416 pp. atlas, 8 pp. + 22 pl.
- CUVIER, G. 1812. Rapport fait à la classe de Sciences mathématiques et physiques, sur divers Cétacés pris sur les côtes de France, principalement sur ceux qui sont échoués près de Paimpol, le 7 janvier 1812. Annales du Muséum d'Histoire Naturelle 1812:1-16 + pl. 1.
- CUVIER, G. 1823. Recherches sur les ossements fossiles. Vol. 5. G. Dufour et E. d'Octagne, Paris and Amsterdam. 405 pp. + 26 pl.
- CUVIER, G. 1829. Le règne animal. Vol. 1. Deterville. Paris. 584 pp.
- DAILEY, M. D., AND K. A. OTTO. 1982. Parasites as biological indicators of the distributions and diets of marine mammals common to the eastern Pacific. Southwest Fisheries Center Administrative Report LJ-82-13C, Southwest Fisheries Center, La Jolla, CA. 44 pp.
- DAILEY, M. D., AND W. F. PERRIN. 1973. Helminth parasites of porpoises of the genus *Stenella* in the eastern tropical Pacific, with descriptions of two new species: *Mastigonema stenellae* gen. et sp. n. (Nematoda: Spiruroidea) and *Zalophotrema pacificum* sp. n. (Trematoda: Digenea). Fishery Bulletin 71:455-471.
- DALL, W. H. 1874. Catalogue of the Cetacea of the North Pacific Ocean, with osteological notes, and descriptions of some new forms; with reference to the forms described and figured in the foregoing monograph of Pacific Cetacea, by Captain C. M. Scammon, U.S.R.M. Pages 281-308 appended to C. M. Scammon. The marine mammals of the north-western coast of North America, described and illustrated: together with an account of the American whale-fishery. John H. Carmany, San Francisco, and G. P. Putnam's Sons, New York, NY.
- DIXON, W. J., ED. 1985. BMDP statistical software. University of California Press, Berkeley, Los Angeles and London. 732 pp.
- DOUGLAS, M. E., G. D. SCHNELL AND D. J. HOUGH. 1984. Differentiation between inshore and offshore spotted dolphins in the eastern tropical Pacific Ocean. Journal of Mammalogy 65:375-387.
- DUFFIELD, D. A. 1977. Phylokaryotypic evolution of the Cetacea. Ph.D. Dissertation, University of California, Los Angeles. 154 pp.
- DUPUY, A. R., AND J. MAIGRET. 1976. Les mammifères marins des côtes du Sénégal. 1. Bilan des observations signalées, entre 1960 et 1976. Bulletin de l'Institut Fondamental d'Afrique Noire 38, ser. A:921-928.
- DUPUY, A. R., AND J. MAIGRET. 1978. Les mammifères marins des côtes du Sénégal. 2. Observations signalées en 1977. Bulletin de l'Institut Fondamental d'Afrique Noire 40, Ser. A:457-465.
- ELLERMAN, J. R., AND T. C. S. MORRISON-SCOTT. 1951. Checklist of Palaearctic and Indian mammals 1758-1946. British Museum (Natural History), London. 810 pp.
- ERDMAN, D. S., J. HARMS AND M. M. FLORES. 1973. Cetacean records from the northeastern Caribbean region. Cetology 17. 14 pp.
- FITCH, J. E., AND R. L. BROWNELL, JR. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. Journal of the Fisheries Research Board of Canada 25:2561-2574.
- FOLLETT, W. I., AND L. J. DEMPSTER. 1960. First records of the echeneid fish *Remilegia australis* (Bennett) from California, with meristic data. Proceedings of the California Academy of Sciences 31:169-184.
- FRASER, F. C. 1950. Description of a dolphin *Stenella frontalis* (Cuvier) from the coast

- of French Equatorial Africa. Pages 61–84 and plates 6–9 in *Atlantide Report No. 1. Scientific results of the Danish Expedition to the coasts of tropical West Africa 1945–1946*. Danish Science Press, Copenhagen.
- FRASER, F. C. 1966. Comments on the Delphinoidea. Pages 7–31 in K. S. Norris, ed. *Whales, dolphins, and porpoises*. University of California Press, Berkeley and Los Angeles.
- FRITTS, T. H., AND R. P. REYNOLDS. 1981. Pilot study of the marine mammals, birds and turtles in OCS areas of the Gulf of Mexico. FWS/OBS–81/36. Office of Biological Services, Fish and Wildlife Service, U.S. Department of the Interior, Washington, D.C. 142 pp.
- FRITTS, T. H., A. B. IRVINE, R. D. JENNINGS, L. A. COLLUM, W. HOFFMAN AND M. A. MCGHEE. 1983. Turtles, birds, and mammals in the northern Gulf of Mexico and nearby Atlantic waters. FWS/OBS–82/65. Office of Biological Services, Fish and Wildlife Service, U.S. Department of the Interior, Washington, D.C. 456 pp.
- GRAY, J. E. 1843. List of the specimens of Mammalia in the collections of the British Museum. Trustees of the British Museum, London. 216 pp.
- GRAY, J. E. 1846. On the cetaceous animals. Pages 13–53 in J. Richardson and J. E. Gray, eds. *The zoology of the voyage of H.M.S. Erebus and Terror*. Vol. 1. Mammalia, Birds. Longmans, Brown, Green and Longmans, London.
- GRAY, J. E. 1866. Description of three species of dolphins in the free museum at Liverpool. *Proceedings of the Zoological Society of London* 1865:735–739.
- GUNTER, G. 1941. A record of the long-snouted dolphin, *Stenella plagiodon* (Cope), from the Texas coast. *Journal of Mammalogy* 22:447–448.
- HALL, E. R. 1981. *The mammals of North America*. Vol. II. John Wiley and Sons, New York, Chichester, Brisbane and Toronto. 1181 + 90 pp.
- HERSHKOVITZ, P. 1966. Catalog of living whales. *United States National Museum Bulletin* 246. 259 pp.
- HOHN, A. A., S. J. CHIVERS AND J. BARLOW. 1985. Reproductive maturity and seasonality of male spotted dolphins, *Stenella attenuata*, in the eastern tropical Pacific. *Marine Mammal Science* 1:273–293.
- HOMBRON, J. B., AND H. JACQUINOT. 1842–1853. *Voyage au Pôle Sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée*. Atlas. Mammifères. Gide and Baudry, Paris, issued in unpaginated sections.
- HOMBRON, J. B., AND H. JACQUINOT. 1853. *Voyage au Pôle Sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée*. Zoologie, Vol. 3. Gide and Baudry, Paris. 329 pp.
- HONACKI, J. H., K. E. KINMAN AND J. W. KOEPL, EDS. 1982. *Mammal species of the world: a taxonomic and geographic reference*. Allen Press and The Association of Systematics Collections, Lawrence, KS. 694 pp.
- KASUYA, T. 1985. Effect of exploitation on reproductive parameters of the spotted and striped dolphins off the Pacific coast of Japan. *Scientific Reports of the Whales Research Institute, Tokyo* 36:107–138.
- KELLOGG, R. 1940. Whales, giants of the seas. *National Geographic Magazine*, January:35–90.
- LEGENDIJK, P. 1984. Report of a study of the present status of humpback whales around the Cape Verde Islands, March 1984. Meeting document SC/36/PS16. International Whaling Commission, The Red House, Station Road, Histon, Cambridge, United Kingdom. 8 pp.
- LANG, T. G., AND K. PRYOR. 1966. Hydrodynamic performance of porpoises (*Stenella attenuata*). *Science* 152:531–533.
- LEATHERWOOD, S., D. K. CALDWELL AND H. E. WINN. 1976. Whales, dolphins, and porpoises of the western North Atlantic. National Oceanic and Atmospheric Administration Technical Report NMFS Circular 396. National Marine Fisheries Service, Seattle, WA. 176 pp.

- LEATHERWOOD, J. S., W. F. PERRIN, R. L. GARVIE AND J. C. LA GRANGE. 1973. Observations of sharks attacking porpoises (*Stenella* spp. and *Delphinus* cf. *D. delphis*). Naval Undersea Center Technical Note 908, Naval Undersea Center [Naval Ocean Systems Center], San Diego, CA. 7 pp.
- LEATHERWOOD, S., R. R. REEVES AND L. FOSTER. 1983. The Sierra Club handbook of whales and dolphins. Sierra Club Books, San Francisco, CA. 302 pp.
- LEATHERWOOD, S., R. R. REEVES, W. F. PERRIN AND W. E. EVANS. 1982. Whales, dolphins, and porpoises of the eastern North Pacific and adjacent Arctic waters. National Oceanic and Atmospheric Administration Technical Report Circular 444. National Marine Fisheries Service, Seattle, WA. 245 pp.
- LESSON, R. P., AND P. GARNOT. 1826. Zoologie. Vol. 1, Part 1 in L. I. Duperrey, ed. Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de Sa Majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825. Arthus Bertrand, Paris. 360 pp.
- LEUNG, Y.-K. 1970. First record of the whale-louse genus *Syncyamus* (Cyamidae: Amphipoda) from the western Mediterranean, with notes on the biology of odontocete cyamids. Investigations on Cetacea 2:243-247.
- LÖNNBERG, E. 1934. *Prodelphinus graffmani* n. sp. a new dolphin, from the Pacific coast of Mexico. Arkiv för Zoologi 26A (19). 11 pp. + 1 pl.
- LOWERY, G. H. 1974. The mammals of Louisiana and its adjacent waters. Louisiana State University Press, Baton Rouge. 565 pp.
- LÜTKEN, C. F. 1889. Bidrag til Kundskab om de tre pelagiske Tandhval-Slaegter *Steno*, *Delphinus* og *Prodelphinus*. Spolia Atlantica, Copenhagen. 64 pp.
- MAHNKEN, T., AND R. M. GILMORE. 1959. Suckerfish on porpoise. Journal of Mammalogy 41:134.
- MALM, A. W. 1871. Hvaldjur i Sveriges Museer, Ar 1869. Kongliga Svenska Vetenskaps-Akademiens Handlingar 9(2). 110 pp.
- MERCER, M. C. 1973. Observations on distribution and intraspecific variation patterns of odontocete Cetacea in the western North Atlantic. Journal of the Fisheries Research Board of Canada 30:1111-1130.
- MILLER, G. S., JR., AND R. KELLOGG. 1955. List of North American recent mammals. United States National Museum Bulletin 205. 954 pp.
- MINASIAN, S. M., K. C. BALCOMB AND L. FOSTER. 1984. The world's whales. Smithsonian Books, Washington, D.C. 224 pp.
- MITCHELL, E. 1970. Pigmentation pattern evolution in delphinid cetaceans: an essay in adaptive coloration. Canadian Journal of Zoology 48:717-740.
- MITCHELL, E., ED. 1975. Report of the meeting on smaller cetaceans. Montreal, April 1-11, 1974. Journal of the Fisheries Research Board of Canada 32:889-983.
- MIYAZAKI, N., T. KASUYA AND M. NISHIWAKI. 1974. Distribution and migration of two species of *Stenella* in the Pacific coast of Japan. Scientific Reports of the Whales Research Institute, Tokyo 26:227-243.
- MOORE, J. C. 1953. Distribution of marine mammals to Florida waters. American Midland Naturalist 49:117-158.
- MÖRZER BRUYN, W. F. J. 1971. Field guide of whales and dolphins. Mees, Amsterdam. 258 pp.
- MURPHY, G. 1979. Discover the dolphin. Skin Diver, August:57-59.
- MURPHY, R. C. 1947. Logbook for Grace. Macmillan, New York, NY. 290 pp.
- MYRICK, A. C., JR., A. A. HOHN, J. BARLOW AND P. A. SLOAN. 1986. Reproductive biology of female spotted dolphins, *Stenella attenuata*, from the eastern tropical Pacific. Fishery Bulletin 84:247-259.
- NEILAND, K. A., D. W. RICE AND B. L. HOLDEN. 1970. Helminths of marine mammals. 1. The genus *Nasitrema*, air sinus flukes of delphinid Cetacea. Journal of Parasitology 56:305-316.
- NICHOLS, J. T. 1920. Red bat and spotted porpoise off the Carolinas. Journal of Mammalogy 1:87.

- NISHIWAKI, M. 1967. Distribution and migration of marine mammals in the North Pacific area. Bulletin of the Ocean Research Institute of the University of Tokyo 1: 1-64.
- NISHIWAKI, M. 1972. General biology. Pages 3-204 in S. H. Ridgway, ed. Mammals of the sea. Thomas, Springfield, Illinois.
- NISHIWAKI, M., M. NAKAJIMA AND T. KAMIYA. 1965. A rare species of dolphin (*Stenella attenuata*) from Arari, Japan. Scientific Reports of the Whales Research Institute, Tokyo 19:53-64 + pl. 1-6.
- NORRIS, K. S., ED. 1961. Standardized methods for measuring and recording data on the smaller cetaceans. Journal of Mammalogy 42:471-476.
- OGAWA, T. 1936. Studien ueber die Zahnwale in Japan. (I. Mitteilung.) Syokubutu Oyobi Doburu, Tokyo. 14 pp.
- DE OLIVEIRA GOMES, L. A. 1984. Análise sobre a ocorrência de *Tursiops* sp. na região do Arraial do cabo, Rio de Janeiro, Brasil [abstract]. Primera Reunion de trabajos de Expertos en Mamíferos Acuáticos de America del Sur, Buenos Aires, 25-29 Junio, 1984. Resúmenes:30.
- OLIVER, W. R. B. 1922. A review of the Cetacea of the New Zealand seas. Proceedings of the Zoological Society of London 1922:557-585, pl. 1-4.
- PEALE, T. R. 1848. United States Exploring Expedition. Vol. 8. Mammalia and ornithology. Sherman, Philadelphia. 338 pp.
- PERNETY, A. J. 1769. Journal historique d'un voyage fait aux Îles Malouines en 1763 & 1764 . . . : I-XVI, 3-403, 404-704 + 47, 16 pl. Etienne de Bourdeaux, Berlin.
- PERRIN, W. F. 1969. The barnacle, *Conchoderma auritum*, on a porpoise (*Stenella graffmani*). Journal of Mammalogy 50:149-151.
- PERRIN, W. F. 1970. Color pattern of the eastern Pacific spotted porpoise *Stenella graffmani* Lönnberg (Cetacea, Delphinidae). Zoologica 54:135-142, pl. 1-7.
- PERRIN, W. F. 1972. Color patterns of spinner porpoises (*Stenella* cf. *S. longirostris*) of the eastern Pacific and Hawaii, with comments on delphinid pigmentation. Fishery Bulletin 70:983-1003.
- PERRIN, W. F. 1975. Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern tropical Pacific and Hawaii. Bulletin of the Scripps Institution of Oceanography of the University of California 21. 206 pp.
- PERRIN, W. F. 1985a. The former dolphin fishery at St. Helena. Reports of the International Whaling Commission 35:423-428.
- PERRIN, W. F. 1985b. Patterns of geographical variation in small cetaceans. Zoologica Fennica 172:137-140.
- PERRIN, W. F., J. M. COE AND J. R. ZWEIFEL. 1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fishery Bulletin 74:229-269.
- PERRIN, W. F., W. E. EVANS AND D. B. HOLTS. 1979. Movements of pelagic dolphins (*Stenella* spp.) in the eastern tropical Pacific as indicated by results of tagging, with summary of tagging operations, 1969-76. National Oceanic and Atmospheric Administration Technical Report NMFS SSRF-737. 13 pp.
- PERRIN, W. F., E. D. MITCHELL, J. G. MEAD, D. K. CALDWELL AND P. J. H. VAN BREE. 1981. *Stenella clymene*, a rediscovered tropical dolphin of the Atlantic. Journal of Mammalogy 62:583-598.
- PERRIN, W. F., E. D. MITCHELL AND P. J. H. VAN BREE. 1978. Historical zoogeography of tropical pelagic dolphins (abstract). Page 73 in R. Obrtel, C. Folk and J. Pellantová, eds. II. Congressus Theriologicus Internationalis. Brno. June 20-27, 1978. Abstracts of papers.
- PERRIN, W. F., AND M. J. PERRIN. 1985. Investigation of the cetacean fauna and former dolphin fishery of St. Helena. National Geographic Society Research Reports 21:355-360.
- PERRIN, W. F., AND S. B. REILLY. 1984. Reproductive parameters of dolphins and

- small whales of the family Delphinidae. Report of the International Whaling Commission (Special Issue 6):97-133.
- PERRIN, W. F., W. D. SCOTT, G. J. WALKER AND V. L. CASS. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. National Oceanic and Atmospheric Administration Technical Report NMFS 28. 28 pp.
- PERRIN, W. F., P. A. SLOAN AND J. R. HENDERSON. 1979. Taxonomic status of the 'southwestern stocks' of spinner dolphin *Stenella longirostris* and spotted dolphin *S. attenuata*. Report of the International Whaling Commission 29:175-184.
- PERRIN, W. F., R. R. WARNER, C. H. FISCUS AND D. B. HOLTS. 1973. Stomach contents of porpoise, *Stenella* spp., and yellowfin tuna, *Thunnus albacares*, in mixed-species aggregations. Fishery Bulletin 71:1077-1092.
- PERRYMAN, W. L., AND T. C. FOSTER. 1980. Preliminary report on predation by small whales, mainly the false killer whale, *Pseudorca crassidens*, on dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific. Southwest Fisheries Center Administrative LJ-80-05, Southwest Fisheries Center, La Jolla, CA. 9 pp.
- PINEDO, M. C., AND H. P. CASTELLO. 1980. Primeros registros dos golfinhos *Stenella coeruleoalba*, *Stenella* cf. *plagiodon* e *Steno bredanensis* para o sul do Brasil, com notas osteológicas. Boletim do Instituto de Oceanográfico, São Paulo 29:313-317.
- PUCHERAN, J. 1856. Notices mammalogiques. Revue et Magasin de Zoologie Pure et Appliquée. Second Series, Vol. 8:362-369.
- RAPP, W. 1837. Die Cetaceen zoologisch-anatomisch dargestellt. J. G. Cotta'schen Buchhandlung, Stuttgart and Tuebingen. 182 pp. + 8 pl.
- ROBINEAU, D., AND J.-M. ROSE. 1984. Les Cétacés de Djibouti. Bilan des connaissances actuelles sur la faune cérolgique de la mer Rouge et du golfe d'Aden. Bulletin du Muséum National d'Histoire Naturelle, Paris, Fourth Series, Vol. 6, Section A, 1: 219-249.
- ROSS, G. J. B. 1977. The taxonomy of bottlenosed dolphins *Tursiops* species in South African waters, with notes on their biology. Annals of the Cape Provincial Museums (Natural History) 11:135-194.
- ROSS, G. J. B. 1984. The smaller cetaceans of the south east coast of southern Africa. Annals of the Cape Provincial Museums (Natural History) 15:173-410.
- SCHÉVILL, W. E., AND W. A. WATKINS. 1962. Whale and porpoise voices. A phonograph record. Woods Hole Oceanographic Institution, Woods Hole, MA. Phonograph disk + 24 pp.
- SCHLEGEL, H. 1841. Abhandlungen aus dem Gebiete der Zoologie und vergleichenden Anatomie. Vol. 1. A. Arnz, Leiden. 44 pp. + 6 pl.
- SCHMIDLY, D. J. 1972. First record of Cuvier's dolphin from the Gulf of Mexico with comments on the taxonomic status of *Stenella frontalis*. Journal of Mammalogy 53: 625-628.
- SCHMIDLY, D. J. 1981. Marine mammals of the southeastern United States coast and the Gulf of Mexico. FWS/OBS-80/41. Office of Biological Services, Fish and Wildlife Service, U.S. Department of the Interior, Washington, D.C. 166 pp.
- SCHMIDLY, D. J., AND S. H. SHANE. 1978. A biological assessment of the cetacean fauna of the Texas coast. United States Marine Mammal Commission Report MMC-74/05. United States Marine Mammal Commission, 1625 I Street, N.W., Washington, D.C. 38 pp.
- SCHNELL, G. D., M. E. DOUGLAS AND D. J. HOUGH. 1985. Sexual dimorphism in spotted dolphins (*Stenella attenuata*) in the eastern tropical Pacific Ocean. Marine Mammal Science 1:1-14.
- SCHNELL, G. D., M. E. DOUGLAS AND D. J. HOUGH. 1986. Geographic patterns of variation in spotted dolphins (*Stenella attenuata*) of the eastern tropical Pacific Ocean. Marine Mammal Science 2:186-213.
- VON SCHREBER, J. C. D. 1840. Die Säugethiere. Erlangen, Leipzig [not seen; see Wagner 1846 below].

- SCIENTIFIC EVENT ALERT NETWORK. 1975-1982. SEAN Bulletin 1-7. Natural Museum of Natural History, Smithsonian Institution, Washington, D.C. Various pagination.
- SCOTT, M. D., W. L. PERRYMAN AND W. G. CLARK. 1985. The use of aerial photographs for estimating school sizes of cetaceans. Inter-American Tropical Tuna Commission Bulletin 18:381-419.
- SHANE, S. H. 1977. The population biology of the Atlantic bottlenose dolphin, *Tursiops truncatus*, in the Aransas Pass area of Texas. M.S. dissertation, Graduate College, Texas A & M University, Corpus Christi. 239 pp.
- SHOMURA, R. S., AND T. S. HIDA. 1965. Stomach contents of a dolphin caught in Hawaiian waters. Journal of Mammalogy 46:500-501.
- SMITH, T. D. 1983. Changes in size of three dolphin (*Stenella* spp.) populations in the eastern tropical Pacific. Fishery Bulletin 81:1-13.
- SPRINGER, S. 1957. Some observations on the behavior of schools of fishes in the Gulf of Mexico and adjacent waters. Ecology 38:166-171.
- SUTHERLAND, D. L., AND L. L. MAY. 1977. Spotted dolphins, *Stenella plagiodon* (Cope): underwater observations using an unmanned submersible. Cetology 27. 9 pp.
- TARUSKI, A. G., AND H. E. WINN. 1976. Winter sightings of odontocetes in the West Indies. Cetology 22. 12 pp.
- TROUESSART, E. L. 1898. Catalogus mammalium tam viventium quam fossilium. Pages 1004-1264 in Fasciculus 5. Sirenia, Cetacea, Edentata, Marsupalia, Allotheria, Monotremata. R. Friedlaender and Sohn, Berlin.
- TROUESSART, E. L. 1904-1905. Catalogus mammalium tam viventium quam fossilium. Fifth supplement. R. Friedlaender und Sohn, Berlin. 929 pp.
- TRUE, F. W. 1885. IV.—On a spotted dolphin apparently identical with the *Prodelphinus doris* of Gray. Annual Report of the Board of Regents of the Smithsonian Institution 1884 (Part II):317-324.
- TRUE, F. W. 1889. Contributions to the natural history of the cetaceans. A review of the family Delphinidae. The United States National Museum Bulletin 36. 191 pp. + 47 pl.
- TRUE, F. W. 1894. Notes on some skeletons and skulls of porpoises of the genus *Prodelphinus*, collected by Dr. W. L. Abbott in the Indian Ocean. Proceedings of the United States National Museum 17:33-37.
- WAGNER, J. A. 1846. [Revision of] J. C. D. von Schreber. Die Saeugthiere. Vol. 7. Die Ruderfuesser und Fischzighthiere. Erlangen, Leipzig. VII + 427 pp.
- WEBER, M. 1923. Die Cetaceen der Siboga-Expedition. Fasciculus 97 in M. Weber and L. F. de Beaufort, eds. Siboga-Expeditie. Uitkomsten op zoologisch, botanisch, oceanographisch en geologisch gebied verzameld in de Oost-Indische Archipel 1899-1900. E. J. Brill, Leiden. 38 pp. + 3 pl.
- WINN, H. E. 1982. A characterization of marine mammals and turtles in the mid- and North Atlantic areas of the U.S. outer continental shelf. Bureau of Land Management, United States Department of the Interior, Washington, D.C. 566 pp. + map.
- WORTHEN, G. L. 1981. Preliminary analysis of the potential for stock assessment of Pacific Ocean delphinids by G and C banding. Southwest Fisheries Center Administrative Report LJ-81-02C. Southwest Fisheries Center, La Jolla, California. 97 pp.
- ZAM, S. G., D. K. CALDWELL AND M. C. CALDWELL. 1971. Some endoparasites from small cetaceans collected in Florida and Georgia. Cetology 2. 11 pp.
- ZHOU, K., Y. LI, W. QIAN AND G. YANG. 1980. Notes on three species of dolphins from the South China Sea and Jiulongjiang River. Oceanologia et Limnologia Sinica 11:306-313 + pl. 1-3 (in Chinese).

Received: June 24, 1986

Accepted: September 24, 1986

APPENDIX 1

Museum and Collection Acronyms

AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum (Natural History), London; CM, Charleston Museum, Charleston, South Carolina; CMNH, Cleveland Museum of Natural History; FTI, Fayetteville Technical Institute, Fayetteville, North Carolina; IFAN, Institut Fondamental d'Afrique Noire, Dakar, Senegal; GM, Goteborg Museum; LACM, Los Angeles County Museum of Natural History; LIZ, Institute of Zoology, Leningrad; MACNBA, Museo Argentino de Ciencias Naturales, Buenos Aires; MCNRS, Museu de Ciências Naturais, Rio Grande do Sul, Brazil; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MLF, Marineland of Florida, St. Augustine; MNHN, Muséum National d'Histoire Naturelle, Paris; MSU, McNeese State University, Lake Charles, Louisiana; NCSM, North Carolina State Museum, Raleigh; NJNU, Nanjing Normal University; NMNS, National Museum of Natural Sciences, Ottawa; NSM, National Science Museum, Tokyo; PANS, Philadelphia Academy of Natural Sciences, Pittsburgh; PEM, Port Elizabeth Museum, Port Elizabeth, South Africa; PML, Public Museum of Liverpool; RMNH, State Museum of Natural History, Leiden; RSMAS, Rosenstiel School of Marine and Atmospheric Science, University of Miami; SAM, South African Museum, Cape Town; SDMNH, San Diego Museum of Natural History; SWFC, Southwest Fisheries Center, La Jolla, California; TCWC, Texas Cooperative Wildlife Collection, Texas A & M University, College Station; TKO, Ocean Science Institute, University of Tokyo*; UBC, University of British Columbia, Vancouver; UF, Florida State Museum, University of Florida, Gainesville; USNM, U.S. National Museum of Natural History, Washington, D.C.; UZMC, Zoologisk Museum, Copenhagen; ZMA, Zoologisch Museum, University of Amsterdam; ZMB, Zoologisches Museum, Berlin; ZMUB, Zoologisk Museum, Universitetet i Bergen, Norway.

* All cetacean specimens now at National Science Museum, Tokyo.

OBSERVATIONS OF AN UNIDENTIFIED BEAKED WHALE (*MESOPLODON* SP.) IN THE EASTERN TROPICAL PACIFIC

ROBERT L. PITMAN

Southwest Fisheries Center,
P.O. Box 271,
La Jolla, California 92038

ANELIO AGUAYO L.

JORGE URBÁN R.

Facultad de Ciencias, UNAM,
Apartado Postal 70-572, C.P. 04510,
México, D.F., México

ABSTRACT

Multiple sightings of a distinctive but unidentified species of beaked whale have been made in the eastern tropical Pacific. The unidentified whale has two color morphs: a conspicuously marked black and white form (judged to be larger), and a uniformly gray-brown form. Maximum length estimates have been 5-5.5 m. Other features include a relatively flat head, with a small, distinct melon; a moderately long beak; and a low, wide-based, triangular dorsal fin. On most animals the trailing edge of the dorsal fin is only slightly falcate and often appears straight. On the black and white morph, a broad white or cream-colored swathe originates immediately posterior to the dorsal surface of the head and runs postero-ventrally on either side of the animal. The prevalence of scarring on the black and white animals suggests sexual dimorphism and that these larger, more conspicuously marked animals are adult males, while the smaller, browner, unscarred animals are females and young. Possibilities for identification include: 1) a well-marked race of a known *Mesoplodon* sp., 2) *Mesoplodon (Indopacetus) pacificus* or 3) an undescribed species.

Key words: *Mesoplodon*, unidentified beaked whale, eastern tropical Pacific.

In this paper we report on multiple sightings of a distinctive but as yet unidentified species of beaked whale from the eastern tropical Pacific (ETP). A morph of this whale that we assume is the adult male (*see below*) is conspicuously marked and eminently identifiable in the field. Despite this, it does not fit the description of any known species of ziphiid. We provide here a field description of the whale, identify its range and comment on its identity.

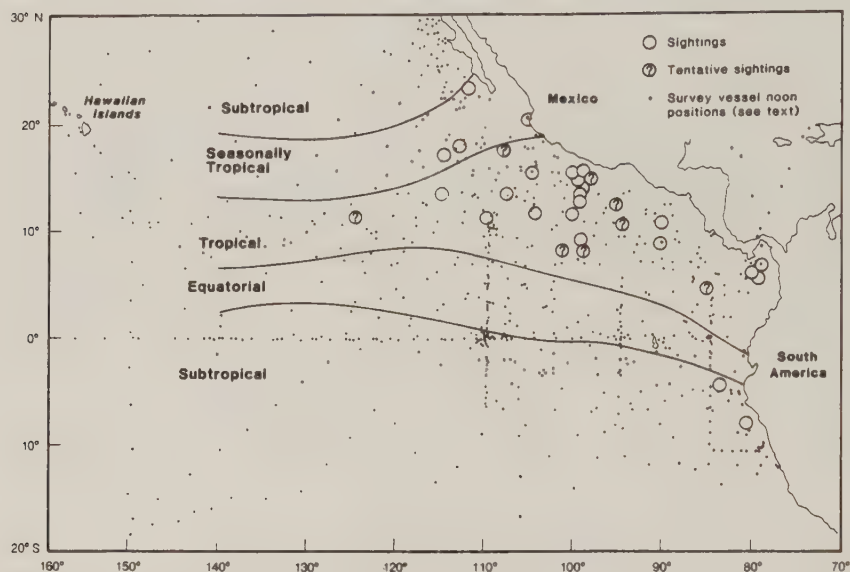


Figure 1. Sightings of the unidentified beaked whale in the eastern tropical Pacific relative to surface water types (after Wyrski 1967).

SIGHTINGS

Figure 1 shows 24 positive and 8 tentative sightings of the unidentified whale. All except one were made by trained observers during marine mammal survey cruises for the Southwest Fisheries Center in the central and eastern tropical Pacific (see Perrin *et al.* 1983). Noon positions of survey vessels during these cruises are also plotted in Figure 1 and indicate the extent of survey coverage. The remaining sighting (Fig. 2) was photographed during a marine mammal identification course taught by two of us (AAL and JUR) at Facultad de Ciencias, Universidad Nacional Autonoma de Mexico (UNAM).

DESCRIPTION

The unidentified whale has two distinct color morphs: a conspicuously marked black and white form and a relatively nondescript morph that appears to be uniformly gray-brown (Figs. 2 and 3). When they have been seen together, the black and white animal has been judged by several observers to be the larger of the two. Estimates of maximum length have most often been between approximately 5–5.5 m, making it an average-to-slightly-large-sized *Mesoplodon* (see Mead 1984).

The head is relatively flat, as in most mesoplodonts, with a small but distinct melon. The beak is moderately long, appearing similar in size to that of *M. densirostris*. On one occasion an observer reported that the mandible was paler than the upper part of the beak on one of the black and white animals.



Figure 2. Photographs of the unidentified beaked whale from Bahía de Banderas, Jalisco, Mexico. The animal shown in 2a and 2b, foreground, is presumably an adult male; notice the scratches behind the white area. Photos by P. Hernández and J. L. López.

The distinctive dorsal fin is low, wide-based and triangular. On most animals the trailing edge of the fin is only slightly falcate and often appears straight.

Most of the dorsal surface of the black and white form, including the dorsal fin, is dark and has been variously described as blackish, black/brown, chocolate brown or dark olive brown. This is similar to the range in color variation noted for short-finned pilot whales (*Globicephala macrorhynchus*) in the eastern Pacific. Pilot whales in the field are generally described as jet black, but in the ETP they often appear greenish brown. Whether these perceived differences are the result of lighting effects, as seems likely, or some actual physical differences, is not known. For the time being, the unidentified whale is best described as black and white.

On the black and white morph, a broad white or cream-colored swathe originates immediately posterior to the dorsal surface of the head and runs postero-ventrally on either side of the animal. Anteriorly, the swathe is rather broad, maybe 60–90 cm, but appears to taper out toward the trailing end. This swathe has been seen to form a very large and contrasting chevron when the animal is viewed head on (and probably from above also). When seen at a distance, the posterior edge of this chevron forms a fairly distinct, contrasting border against the dark color of the rest of the postero-dorsal surface of the whale. On closer inspection however, this border is seen to be broken up by what appears to be white dappling on a dark background. A possible clue concerning the ontogeny of the chevron pattern came from a sighting of an animal, apparently a young adult, that had the contrasting white chevron pattern described above, but it was formed entirely of individual white spots. The white spotting may become confluent as the animal matures, eventually forming the characteristic chevron pattern. The head and beak area of the black and white animal is darker than the chevron but lighter than the back and usually appears reddish brown or tan (Fig. 2).

Whenever the black and white animal has been seen at relatively close range, scratches and scarring have been noted, particularly along the trailing edge of the chevron (*see* Fig. 2). No scars have been seen on the lighter brown animals. In most species of *Mesoplodon*, only adult males have teeth that erupt from the surface of the gum (usually one on either side of the lower jaw). These teeth generally protrude as tusks and, because of intraspecific fighting, males scar each other up considerably at times. Consequently, adult males are often discernable from females and young by the presence of extensive scarring (Heyning 1984). The prevalence of scarring on the black and white animals suggests that the unidentified beaked whale is sexually dimorphic and that the larger, more conspicuously marked black and white animals are adult males, while the smaller, browner, unscarred animals are females and young.

The second, ostensibly female, color form appears uniform gray/brown or bronze-colored. No conspicuous color pattern, markings or scarring have been noticed on this form. The dorsal fin of the brown animal is also low, wide-based and triangular, although it tends to be slightly more falcate than in the males. The brown animals are relatively nondescript and separating them from other mesoplodonts in the field may not be possible. In fact, all of the positive sightings shown in Figure 1 were based on the presence of at least one readily identifiable adult male of the species.

Mead *et al.* (1982) described a similar sexual dimorphism with respect to external color patterns in *M. carlhubbsi*. In that species, the adult male has a "brilliant white" rostrum and a "distinctive white patch . . . centered on the dorsal prominence of the melon," while the remainder of the body is dark gray or black. Female and subadult *M. carlhubbsi* show an incipient version of this pattern but are more uniformly gray-brown.

Figure 3 is an artist's rendition of both morphs of the unidentified whale based on photographs (Fig. 2), and descriptions and sketches made during field observations. The ventral color patterns shown are inferential, as that part of



Figure 3. An artist's depiction of the unidentified beaked whale drawn from Figure 2 and illustrations and descriptions made in the field. The larger animal is a presumed male, while the smaller animal (not to scale) shows the pattern of presumed female/juveniles (*see text*). We have seen little more of this animal than is visible in Figure 2 and the ventral patterns shown here are inferred. Illustration by Lou Silva.

the animal has never been seen. Likewise, the shape of the beak and gape line has not been adequately examined; the illustration shows a generalized mesopodont head and rostrum of about the right proportions for the unidentified species.

No erupted teeth have been seen on this species either, though we have specifically looked for them. We suspect if they exist, and they almost certainly do, they are probably not as large or conspicuous as in *M. layardii* or even *M. carlhubbsi*.

DISTRIBUTION

The normal range of the unidentified whale appears to be restricted to the eastern tropical Pacific (Fig. 1). Nearly all of our sightings were within an area Wyrtki (1967) characterized as tropical surface water. This is an area of very warm water and recorded sea surface temperatures for 20 of our sightings were $\geq 27^{\circ}\text{C}$ (80°F). The two sightings in Figure 1 that appear south of this range were associated with southerly intrusions of warm water. The southernmost sighting was made in February 1983 when a major El Niño event was shifting anomalously warm water and associated organisms south along the coast of Peru (Barber and Chavez 1983, Velez *et al.* 1984).

BIOLOGICAL OBSERVATIONS

Herd size for the 24 positive sightings ranged from 1 to 8, with groups of 2 or 3 being the most common. As noted above however, these results pertain

only to sightings with adult males present. For 16 sightings where color morph information was obtained for all of the animals present, 5 were lone males, 6 were male/female (or possibly male/juvenile) pairs, and 5 involved single males with 2 or more female/juveniles, including one sighting with an estimated 8 animals.

At sea, this whale behaves similarly to other *Mesoplodon* species. It is usually seen rolling over slowly at the surface or traveling at a moderate pace and in fairly tight groups when more than one animal is present. It generally does not engage in any sort of "playful" activity, *e.g.*, breaching, tail-slapping, or spy-hopping, though on one occasion a lone male was seen to breach clear of the water three times in a row. Like other members of the genus, its behavior repertoire, at least when it is at the surface, appears to be very limited and stereotyped. Under normal circumstances there is no visible blow.

IDENTITY OF THE WHALE

In considering the possibilities for identification, two genera of beaked whales, *Berardius* and *Hyperoodon*, can be eliminated because of excessive size (approximately 12 and 7 m, respectively). *Ziphius cavirostris* is tan or whitish with a stubby beak and is a species we commonly identify in the eastern tropical Pacific (Pitman, unpublished observations). *Tasmacetus shepherdi* is probably too large also (maximum length at least 7 m, Mead 1984) and its distribution appears to be circumpolar in southern oceans (Gaskin 1982). The relatively small size (5–5.5 m), distinct beak, and small but discernable melon lead us to identify the whale with the genus *Mesoplodon*.

Currently there are 12 recognized living species of *Mesoplodon*. From descriptions and photographs of stranded animals, the external pigmentation patterns of most of these have gradually become known (*e.g.*, Baker 1983, Leatherwood *et al.* 1983), and none matches the description of the unidentified whale. (A possible exception to this, *M. (Indopacetus) pacificus*, is discussed below.)

Nearly all of the information on *Mesoplodon* distribution has come from stranded specimens. Gaskin (1982) stated that the genus "seems to be in a process of prolific speciation, possibly as a result of population isolation events which began in the Pliocene and were completed in the Pleistocene." Given the large number of species in this open ocean group, it is not surprising that the distributions of individual species appear to be limited to distinct water masses (Mead 1981, Mead *et al.* 1982). Of the species known to inhabit tropical or warm temperate waters, *M. europaeus* is known only from the Atlantic, *M. ginkgodens* inhabits the western Pacific (though apparently strays to the eastern Pacific), and *M. densirostris* is pantropical. One of us (RLP) has identified *M. densirostris* several times in the eastern tropical Pacific but only west of the area where the unidentified whale occurs. To date, there has not been any *Mesoplodon* specimen material collected from within the area that appears to be the normal range of the unidentified whale (J. Mead, personal communication).

Tropical surface water and the apparent range of the unidentified whale (Fig. 1) both correspond to a distinct and highly productive oceanographic area that

forms a unique biotic province in the eastern Pacific (Reid 1962, Wyrčki 1967, McGowan 1972, Au and Perryman 1985). The range of the unidentified whale is also nearly identical to the range of the eastern spinner dolphin (*Stenella longirostris*), a pantropical species with a well-marked form endemic to the eastern tropical Pacific (Perrin *et al.* 1985). From the evidence above, it seems likely that a distinct, possibly endemic, species of *Mesoplodon* also occurs in the eastern tropical Pacific.

Possibilities for identification of the unidentified whale include the following:

- 1) It may be a well-marked race of a known species of *Mesoplodon*.
- 2) *Mesoplodon (Indopacetus) pacificus* is currently the rarest extant species of whale known and has never been identified in the flesh. It is known from only two skulls: one from Queensland, Australia, and one from Somalia, northeast Africa. It is possible, however, that these records represent extralimital strays from a localized population inhabiting a little-explored area, such as the eastern tropical Pacific.
- 3) It may be an undescribed species.

The identity of the whale will remain unknown until a stranded specimen is collected.

ACKNOWLEDGMENTS

We would like to thank Jim Cotton, Gary Friedrichsen and Scott Sinclair for their capable assistance in the field. David Au, Jim Mead, John Heyning and especially William Perrin improved the manuscript with their comments. We thank P. Hernández and J. L. López for use of their photographs, Henry Orr for drafting Figure 1, and we gratefully acknowledge the talents of Lou Silva in preparing Figure 3.

LITERATURE CITED

- AU, D. W. K., AND W. L. PERRYMAN. 1985. Dolphin habitats in the eastern tropical Pacific. *Fishery Bulletin*, U.S. 83:623–643.
- BAKER, A. N. 1983. Whales and dolphins of New Zealand; an identification guide. Victoria University Press, Wellington. 133 pp.
- BARBER, R. T., AND F. P. CHAVEZ. 1983. Biological consequences of El Niño. *Science* 222:1203–1210.
- GASKIN, D. E. 1982. The ecology of whales and dolphins, Heinemann, London and Exeter, New Hampshire. 459 pp.
- HEYNING, J. E. 1984. Functional morphology involved in intraspecific fighting of the beaked whale, *Mesoplodon carlhubbsi*. *Canadian Journal of Zoology* 62:1645–1654.
- LEATHERWOOD, S., R. R. REEVES AND L. FOSTER. 1983. The Sierra Club handbook of whales and dolphins. Sierra Club Books, San Francisco. 302 pp.
- MCGOWAN, J. A. 1972. The nature of oceanic ecosystems. Pages 9–28 in C. B. Miller, ed. The biology of the oceanic Pacific. Proceedings of the 33rd Annual Biology Colloquium, Oregon State University Press, Corvallis, Oregon.
- MEAD, J. G. 1981. First records of *Mesoplodon hectori* (Ziphiidae) from the northern hemisphere and a description of the adult male. *Journal of Mammalogy* 62:430–432.
- MEAD, J. G. 1984. Survey of reproductive data for the beaked whales (Ziphiidae). Pages 91–96 in W. F. Perrin *et al.*, eds. Cetacean reproduction: estimating parameters

- for stock assessment and management. Reports of the International Whaling Commission, Special Issue 6.
- MEAD, J. G., W. A. WALKER AND W. J. HOUCK. 1982. Biological observations on *Mesoplodon carlhubbsi* (Cetacea: Ziphiidae). Smithsonian Contributions to Zoology 344. 25 pp.
- PERRIN, W. F., M. D. SCOTT, G. J. WALKER, F. M. RALSTON AND D. W. K. AU. 1983. Distribution of four dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific, with an annotated catalogue of data sources. NOAA Technical Memorandum NMFS-SWFC-38. 65 pp.
- PERRIN, W. F., M. D. SCOTT, G. J. WALKER AND V. L. CASS. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific. NOAA Technical Report NMFS 28. 28 pp.
- REID, J. L., JR. 1962. On circulation, phosphate-phosphorus content, and zooplankton volumes in the upper part of the Pacific. *Limnology and Oceanography* 7:287-306.
- VELEZ, J., J. ZEBALLOS, AND M. MENDEZ. 1984. Effects of the 1982-83 El Niño on the fishes and crustaceans off Peru. *Tropical Ocean-Atmosphere Newsletter* 28: 10-12.
- WYRTKI, K. 1967. Circulation and water masses in the eastern equatorial Pacific Ocean. *International Journal of Oceanology and Limnology* 1:117-147.

Received: March 7, 1986

Accepted: May 11, 1987

RELATIVE ABUNDANCE, DISTRIBUTION AND INTER-SPECIFIC RELATIONSHIP OF CETACEAN SCHOOLS IN THE EASTERN TROPICAL PACIFIC

TOM POLACHECK¹

Southwest Fisheries Center, National Marine Fisheries Service,
La Jolla, California 92038, and
Department of Biology, University of Oregon, Eugene, Oregon 97403

ABSTRACT

The relative abundance of the most common cetacean schools in the eastern tropical Pacific Ocean for 1977-1980 are estimated based on encounter rates with tuna purse-seiners. No temporal trends were apparent in the relative abundance estimates. The geographic distributions for eight different school types are described. Multivariate statistical techniques are used to investigate inter-relations between species and relationships to parameters of the physical environment. The results suggest three major species groupings: (1) an inshore grouping of bottlenose dolphins (*Tursiops truncatus*), Risso's dolphin (*Grampus griseus*), pilot whales (*Globicephala macrorhynchus*) and, to a lesser extent, common dolphins (*Delphinus delphis*); (2) an offshore pelagic grouping of spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*); and (3) an association between pilot whales and common dolphins that overlaps the first grouping in inshore areas and also tends to be segregated from the second grouping. The results also suggest that relative densities of different school types are strongly related to physical environmental parameters, the most important being sea surface temperature, depth of the thermocline and thickness of the oxygen minimum layer.

Key words: abundance, distribution, *Delphinus delphis*, *Globicephala macrorhynchus*, *Grampus griseus*, *Stenella attenuata*, *Stenella longirostris*, *Tursiops truncatus*, multivariate, temperature, thermocline, oxygen minimum.

A large number of cetacean species is known to inhabit the eastern tropical Pacific Ocean (Leatherwood *et al.* 1972). Little is known about the structure of this group of marine mammals or the factors influencing the spatial distribution of its members. A knowledge of the distribution and association between species is central to an understanding of the ecology of any community. Without such knowledge, it is impossible to accurately define the structure of a com-

¹ Present address: Northeast Fisheries Center, National Marine Fisheries Service, Woods Hole, Massachusetts 02543.

munity, much less to address the question of what factors are actually structuring the community and controlling its dynamics. Interest and management concerns about the cetacean species inhabiting the eastern tropical Pacific have developed because of the involvement and incidental killing of some of these species in the purse-seine fishery for yellowfin tuna (*Thunnus albacares*) (Perrin 1968, 1969). A knowledge of the spatial distribution and associations of these cetacean species is important for a complete assessment and management of these species.

Until recently, no reliable information was available on the distributional ranges of many of the major species. As a result of extensive research by the National Marine Fisheries Service into the tuna purse-seine fishery and the incidental involvement of dolphins in the harvesting process, a large body of data has been collected on the more abundant marine mammal species. The distributional ranges of the more abundant species (including distinct morphological races) have been described from this information (Perrin 1975, Perrin *et al.* 1976, 1979, 1983, Holt and Powers 1982). However, uncertainty remains about the boundaries of these ranges, particularly in the far-western and southern portions of the eastern tropical Pacific.

Within these distributional ranges, only a few analyses exist of the distributional patterns of some of the more common species (Reilly 1977, Au *et al.* 1979, Leatherwood *et al.* 1980). Except for Reilly's (1977) study on the relative densities of pilot whales, none of these studies has been based on direct quantitative measures of density. Their primary focus has been to describe the major areas of distribution of one or more species. In addition, Au *et al.* (1979) examine the relationship between environmental variables and the spatial frequency of sightings without regard to searching effort for the four most common dolphin species. The authors note the existence of apparently strong relations between the number of sightings and sea surface temperature, thermocline depth, and areas of frontal convergences. Because of a statistical mistake, Reilly (1977) found no relationship between environmental variables and his measure of relative densities for pilot whales (Reilly, pers. comm.). Scattered within other studies are comments, but no quantitative analyses, on the apparent association of various cetacean species with environmental parameters. The possible inter-relations between species have been discussed only qualitatively (*e.g.*, Au *et al.* 1979, 1980, Au and Pitman 1981).

In this paper, the spatial distribution of the relative densities of schools is estimated and examined for the eight most commonly sighted cetacean species based on encounter rates with tuna purse-seiners. The inter-relations among these spatial distributions and their relations to the general physical environment are explored with multivariate statistical methods.

MATERIALS AND METHODS

The Data

The data used for estimating relative densities in this paper were collected by trained scientific observers from the National Marine Fisheries Service aboard

operating U.S. tuna purse-seiners. These observers collected information on all sightings of marine mammals and on the searching activities of the vessels. Details on the data gathered, the collection procedures and their preparation can be found in Polacheck (1983, 1984) and Perrin *et al.* (1983). The analyses presented below are based on data collected from 1977 to 1980. While data are available from other years, sample sizes are considerably smaller and collection procedures differed in earlier years.

Since the data were gathered aboard working purse-seiners, the sampling distribution of searching effort was not random. Purse-seiners concentrate their effort both seasonally and at relatively fine spatial scales (Polacheck 1983). Also, observers do not generally have access to the 25 $\times$ binoculars used by the crew for searching. For schools sighted at a distance, but not approached by the vessel, positive identifications were usually not made. Thirty-eight percent of the dolphin schools reported were not positively identified by the observer. Schools not identified are probably not random with respect to species (*i.e.*, schools associated with tuna are more likely to be investigated). Both of these factors may induce unknown biases into the results. The problem of non-random search is compensated in part in the analyses below by the fact that all calculations have been performed based on a 5° square stratification of the data. The analyses presented below are dependent upon the relative spatial patterns of the sighting rates and not absolute rates. As such, the problem of unidentified schools should not induce serious bias unless species are selectively non-identified by area. However, the problem of non-identification means that the number of schools sighted is smaller than might be expected for species not involved in the tuna fishery. In these cases, caution should be used in interpreting lack of positive results and relationships. This is particularly true for the striped dolphin, which had the third lowest encounter rate by purse-seiners of the species considered below, but is the most frequently sighted dolphin species on research cruises (Holt and Powers 1982).

School Types

Relative densities for nine types of schools are examined. These represent the eight species most frequently encountered by purse seiners. They are:

1. Schools of spotted dolphins (*Stenella attenuata*)
2. Schools of spinner dolphins (*S. longirostris*)
3. Schools of common dolphins (*Delphinus delphis*)
4. Schools of striped dolphins (*S. coeruleoalba*)
5. Mixed schools of spotted and spinner dolphins (*S. attenuata* and *S. longirostris*)
6. Schools containing bottlenose dolphins (*Tursiops truncatus*)
7. Schools containing Risso's dolphins (*Grampus griseus*)
8. Schools containing pilot whales (*Globicephala macrorhynchus*)
9. Schools containing sperm whales (*Physeter catodon*)

A school was classified as one of the first four types if its estimated composition

contained at least 90 percent of the species referred to. Mixed schools of spotted and spinner dolphins were defined as any school for which the estimated composition contained more than 10 percent for each species. For the last four school types, a school was included if it contained any identified individuals of that species. This was done because the actual number of individuals seen in any single sighting of these four species tends to be small. Thus, even when seen in a mixed school, these animals represent a significant collection of individuals for that species, whereas the frequency of mixed schools of these species was too infrequent to consider separate classifications. For these school types, a few mixed schools may be counted as more than a single type. Common and striped dolphins rarely represented less than 90 percent of a school. Spotted dolphins rarely constituted less than 10 percent of the school. The spinner dolphin was most frequently found as a minor constituent in schools dominated by other species (primarily spotted dolphins). Thus, ~20 percent of all schools containing any spinner dolphins were composed of less than 10 percent of spinner dolphins. However, even for this species, this represents only ~1 percent of all individuals encountered. Although information on species identification was collected from crew members as well as from the observers, only positive identifications made by the observer are used here because of the uncertainty involved in the crew identifications for many of the species.

Calculations and Statistical Methods

The relative densities within a geographic stratum were calculated as the total number of encounters by all vessels divided by the sum of distance searched by all vessels. This is equivalent to the weighted average of the encounter rate for each vessel when the weights are equal to the distance searched by a vessel within a stratum. In Polacheck (1983), the question of appropriate weights is discussed. Estimates of the variance of these relative density estimates within a stratum can be calculated using standard formulae for the variance of a weighted mean (Seber 1973).

In this paper, all calculations are based on 5° square stratifications of the data. This scale was selected because encounter rates tend to be too variable at any finer scale, given the total number of sightings. Similarly, encounter rates were only considered if a minimum of 500 mi of searching was conducted within any stratum in order to remove the variability associated with very small numbers of encounters.

Average annual estimates of the overall encounter rates from 1977 to 1980 for each species were calculated as the simple average of the encounter rates in each 5° square. The method used for estimating the variance of these average annual rates is detailed in Polacheck (1983).

For the common and spinner dolphins, the annual rates were calculated based on their known historical ranges from Holt and Powers (1982). For the other species, these rates were calculated for the area of the known historical range of the spotted dolphin, also from Holt and Powers (1982). This area was chosen because the distributional ranges for most of these other species within

the eastern tropical Pacific are not well known. This area provides a common basis for comparison. Given the lack of searching effort in the western and southern areas of the eastern tropical Pacific (Polacheck 1983), the exact choice of the offshore boundaries tends to be immaterial to the final results. Revised and expanded estimates of these historical ranges have been produced by Perrin *et al.* (1983). In comparison with the ranges provided in Holt and Powers (1982), these revised ranges contain no new areas in which substantial searching by purse-seiners has occurred. These revised ranges were not available at the time when the calculations in this paper were performed. These annual rates were calculated primarily to see if there were any pronounced time trends for any of the species.

Inter-relations among the species were examined initially by calculating the correlation matrix between the encounter rates within a year for all 5° squares south of 25°N and with a minimum of 500 mi searching. An overall correlation matrix was also calculated utilizing the four annual estimates for a 5° square as independent replicates. This overall correlation matrix thus takes into account variation between years.

Factor analyses based on principal components (Kendall 1980) were conducted based on these correlation matrices. The resulting factor loading provides a measure of the association between the relative density estimates. The spatial patterns for the factor scores for each 5° square were examined to see if the implied associations from the factor analyses corresponded to any spatial relationships. Separate factor analyses were done for each year's data as well as an analysis based on the combined correlation matrix. Comparison of the results among these analyses provides an indication of the robustness and consistency of the results. Both weighted and unweighted factor analyses were run. In the weighted analyses, the weights were made equal to the total distance searched within a 5° square to reflect the differences in variances of the estimates owing to differences in search effort. The results were similar for both the weighted and unweighted analyses. Only the results of the unweighted analysis are presented. Rotation of the factor loadings was by the varimax method.

The relationship between the encounter rates and the spatial variation in the oceanic environment was examined for 13 variables. Only scattered information, derived from various sources over various time periods, is available on environmental or climatological conditions in the eastern tropical Pacific. The data that are used here are from the compilation put together by Schnell *et al.* (1982) (modified slightly in Polacheck [1983]). They are neither real-time nor sighting associated measurements. They are meant as a rough measure of the average conditions prevailing in the eastern tropical Pacific. Table 1 lists the variables used and their abbreviations.

To test for any relationship among these environmental variables and the observed encounter rates, a principal component analysis was performed on the 13 environmental variables, followed by a multiple regression analysis of the estimated encounter rate for each school type against these principal components.

Reilly (1977) performed a similar analysis on his estimates of the relative

Table 1. Descriptions and abbreviations of the 13 environmental measurements.

Abbreviation	Description
1. N. Current	Average northerly component of the sea surface current in winter
2. W. Current	Average westerly component of the sea surface current in winter
3. Depth	Average sea depth
4. Jan. Solar Insol.	Average incoming solar radiation for January (g cal/cm)
5. Ann. Solar Insol.	Average annual incoming solar radiation (g cal/cm)
6. Jan. Temp.	Average sea surface temperature in January
7. July Temp.	Average sea surface temperature in July
8. Temp. Var.	Average annual sea surface temperature variation
9. Depth O ₂ Min.	Average depth at which oxygen content of sea water falls below 1.0 ml/l
10. Thick. O ₂ Min.	Thickness of the subsurface layer with an oxygen content of less than 1.0 ml/l
11. Salinity	Average salinity of surface sea water
12. W. Thermocline	Average depth of the mixed layer for January, February and March
13. Thermocline Var.	Average annual variation in the depth of the center of the permanent thermocline

densities of pilot whales. Regression analysis was done on the principal components because large correlations exist between the environmental variables that would make a meaningful interpretation of simple multiple regression analyses on the original data difficult. The principal components are a mutually orthogonal and independent linear combination of the environmental data (Kendall 1980) and the resulting regression parameters are mutually independent. With this method, the independent contribution of each principal component to the variance in the encounter rate is easily assessed while the contribution of each of the environmental variables to any principal component can also be examined for an indication of the most important environmental variables. The order in which components were entered into the analyses was by rank of their correlation with the dependent variable.

The principal components are numbered in order of the amount of the total variance that they explain in the environmental data. As such, by noting which components are important predictors in the regression analyses, one has an indication of whether the major variation in the environment as measured by the independent variables correlates with variation in relative densities as measured by the encounter rates.

The combined set of encounter rates for all four years was used for these regression analyses since the environmental data have no annual component but are only estimates of the average conditions prevailing in the eastern tropical Pacific. This combined data set contains up to four independent estimates of the encounter rate within a 5° square. Thus, these analyses include within them a measure of the variation in the encounter rates between years. The same set of geographic squares that was used in the factor analyses was used in these

regression analyses. The environmental variables were transformed to standardize normal scores before the principal components were calculated in order to reflect relative and not absolute variations.

In addition to the regressions on principal components, a canonical correlation analysis is presented for the relationship between the set of encounter rates for all species and the set of environmental variables. Canonical correlations reduce the dependency between the sets of data to their simplest possible form and provide an indication of the degree of inter-relatedness between them (Pielou 1977, Kendall 1980). Canonical correlation analyses have not been widely used by ecologists although Pielou (1977) suggests that they may be a powerful tool for providing insights into the inter-relation between two sets of ecological variables. The same data sets that were used in the factor analyses and the regression on principal components are used for this canonical correlation analysis. Both sets of variables were transformed to their standardized, normal scores.

RESULTS

Annual Rates

The average annual encounter rates suggest no consistent trend in abundances over the four years of data (Table 2). The amount of variation associated with individual estimates tends to be high (*e.g.*, coefficients of variations between 7 and 20 percent) because of the relative rarity of encounters for many of these school types. The rate for mixed spotted and spinner schools show the most consistent trend (downward), but, given the associated variability and fluctuations in the estimates, no conclusion about temporal changes is warranted. The encounter rates for 1977 are always the highest except for schools containing Risso's dolphins.

Spatial Distributions

For all of the species considered, the spatial density of schools based on these encounter rate estimates is non-uniform throughout the eastern tropical Pacific (Fig. 1). The values in this figure are the weighted averages of the estimated yearly encounter rate within a 5° square where the weights equal the annual distance searched. For the sperm and pilot whales and for the common, bottlenose and Risso's dolphins, high encounter rates tend to be mainly in nearshore areas. For common dolphins and perhaps pilot whales, there appears to be an additional offshore concentration but of considerably lower densities, centered at about 10°N and 135–140°W. Reilly (1977) noted an offshore concentration of pilot whales, describing it as a distinct population center. The inshore distribution for common dolphins are concentrated in two areas at 25°N and 5°N with a hiatus between them. The distribution of almost pure schools of spotted dolphins roughly parallels the distribution pattern for all spotted dolphin schools examined in detail in Polacheck (1983). The distribution of schools of spinner and striped dolphins is more diffuse. Highest encounter rates for schools of

Table 2. Estimates of the average annual encounter rate for nine types of cetacean schools in the eastern tropical Pacific. Encounter rates are number of schools per 1,000 mi of searching. Numbers in parentheses are estimates of the standard deviations (based on equation 2 of Chapter VIII in Polacheck 1983).

Species	1977	1978	1979	1980
Spotted dolphin	5.555 (0.200)	3.631 (0.204)	5.455 (0.250)	3.853 (0.199)
Spinner dolphin	0.899 (0.066)	0.571 (0.104)	0.408 (0.048)	0.609 (0.097)
Mixed spotted/spinner	1.631 (0.090)	1.368 (0.104)	1.369 (0.103)	1.032 (0.098)
Common dolphin	1.177 (0.127)	0.510 (0.043)	1.102 (0.099)	0.673 (0.116)
Striped dolphin	0.378 (0.050)	0.351 (0.042)	0.314 (0.033)	0.408 (0.061)
Bottlenose dolphin	0.876 (0.101)	0.539 (0.043)	0.740 (0.064)	0.581 (0.052)
Risso's dolphin	0.098 (0.036)	0.129 (0.027)	0.112 (0.023)	0.098 (0.023)
Pilot whale	0.878 (0.148)	0.334 (0.030)	0.554 (0.061)	0.507 (0.066)
Sperm whale	0.324 (0.032)	0.258 (0.024)	0.362 (0.050)	0.276 (0.030)
No. of 5° squares ^a	44	45	42	41
Total distance searched (mi)	435,808	487,956	354,555	224,148

^a Number of squares and total distance searched vary slightly for common and spinner dolphins because of the different areas used to define the boundaries for these two species.

striped dolphins are found southwest of the Galapagos and for pure schools of spinner dolphins, off western Mexico. The lack of a stronger pattern may be due partially to the poor resolution in the data because of the overall low encounter rates for these two species. The distribution of mixed schools of spotted and spinner dolphins is also diffuse, but their encounter rates tend to be highest in the offshore area around 10°N.

Spatial Relations between Species

The estimates of the correlation coefficient for the encounter rates within a 5° square between species suggest that relatively strong associations in densities between species may exist (Table 3). These correlation coefficients can be considered minimal estimates, given the large sampling error associated with the individual encounter rate estimates.

When factor analyses are used to classify these associations between species, the results suggest two or three main species groupings. Factor analysis on the correlation matrix for the encounter rates for all four years' combined data

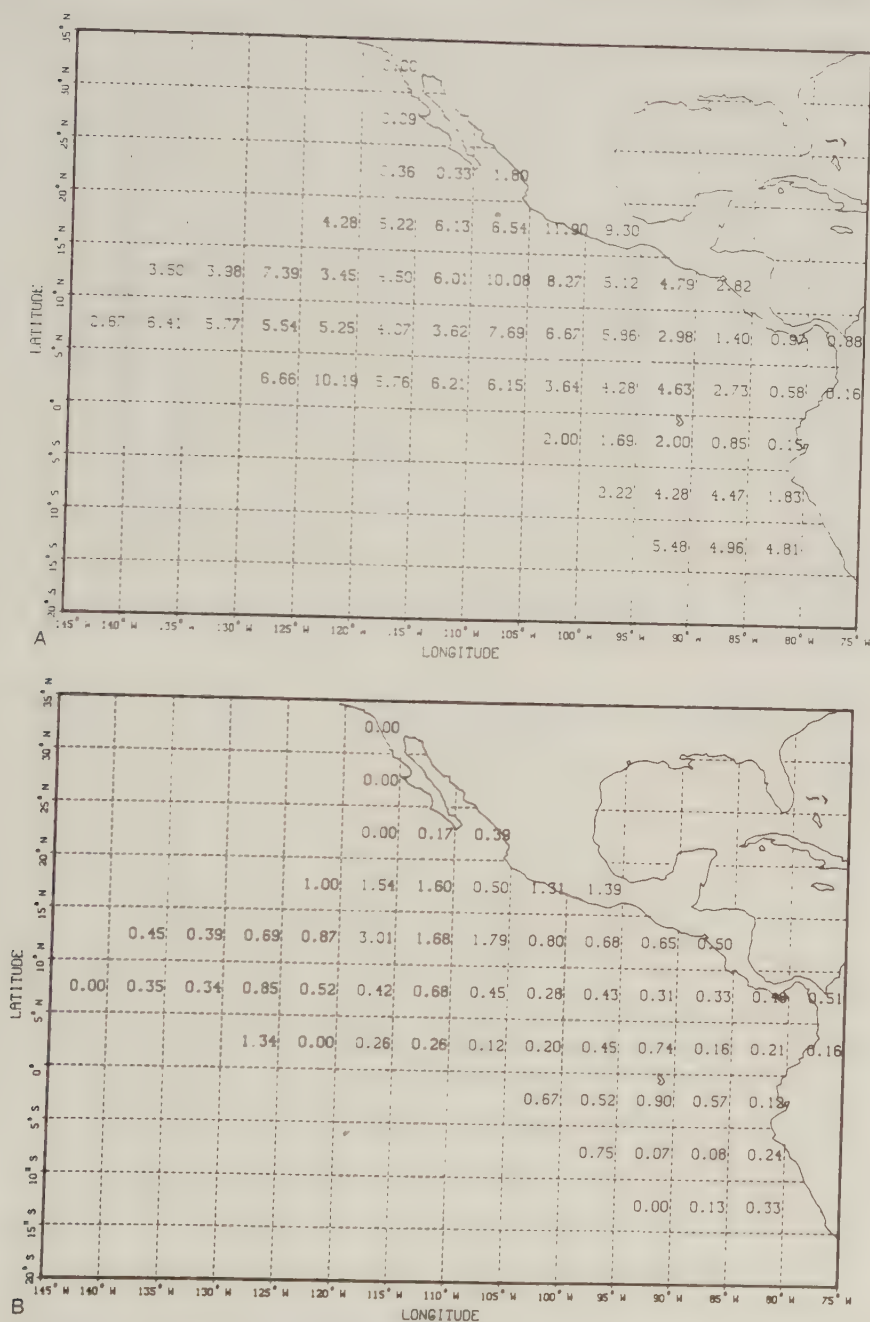


Figure 1. Weighted average estimates of the annual encounter rates (number of schools/1,000 mi searched) from 1977–1980 by 5° squares for marine mammal schools in the eastern tropical Pacific. (A) Pure spotted dolphin schools. (B) Pure spinner dolphin schools.

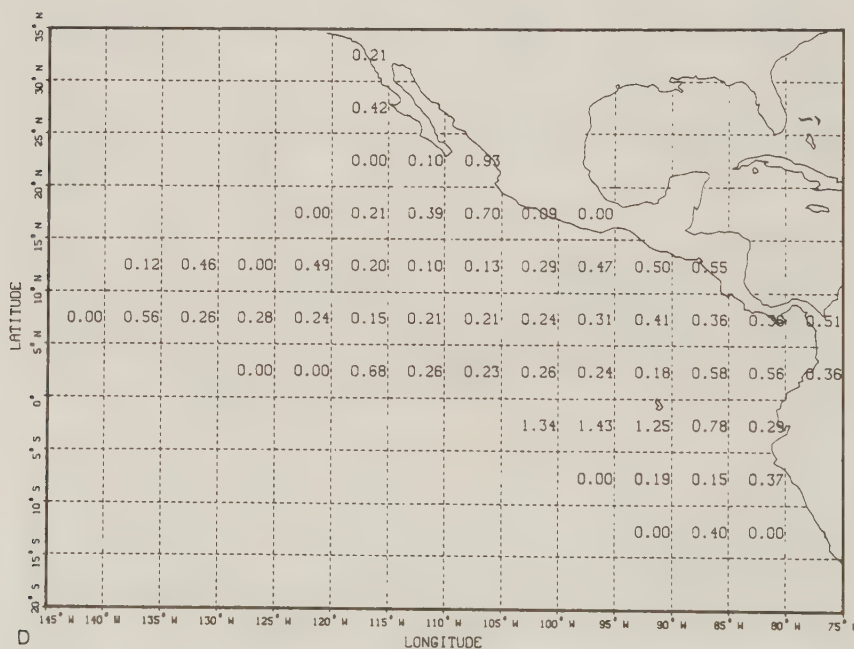
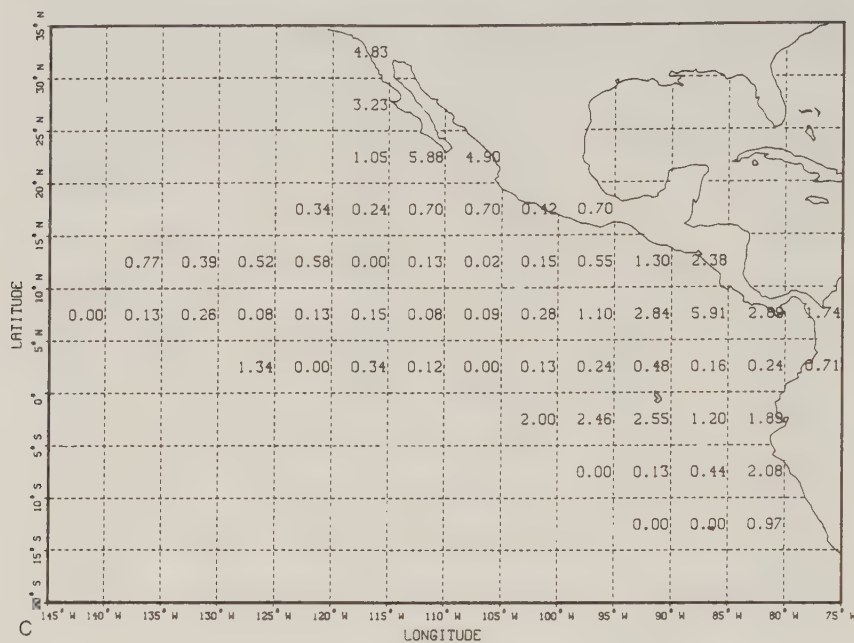


Figure 1. Continued. Weighted average estimates of the annual encounter rates (number of schools/1,000 mi searched) from 1977–1980 by 5° squares for marine mammal schools in the eastern tropical Pacific. (C) Pure common dolphin schools. (D) Pure striped dolphin schools.

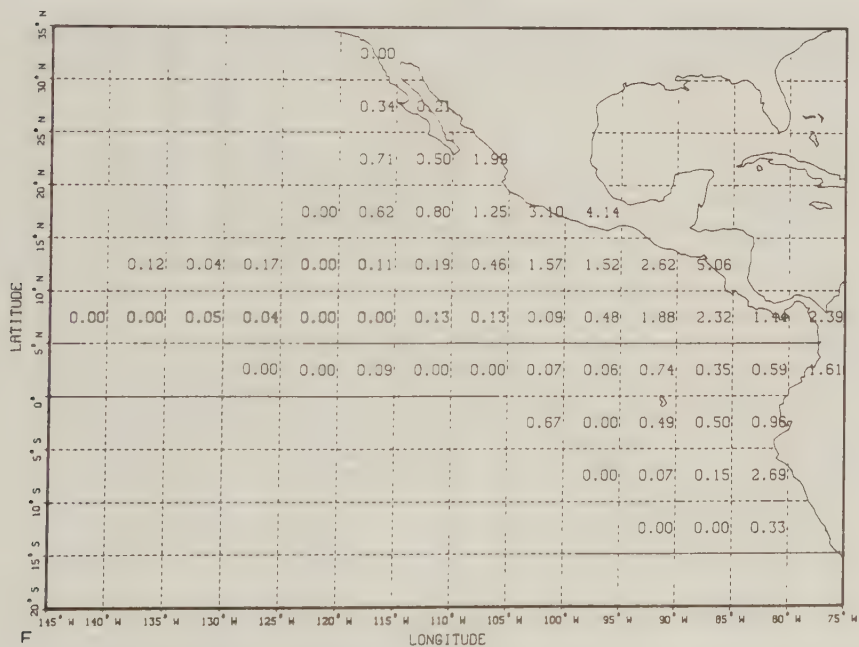
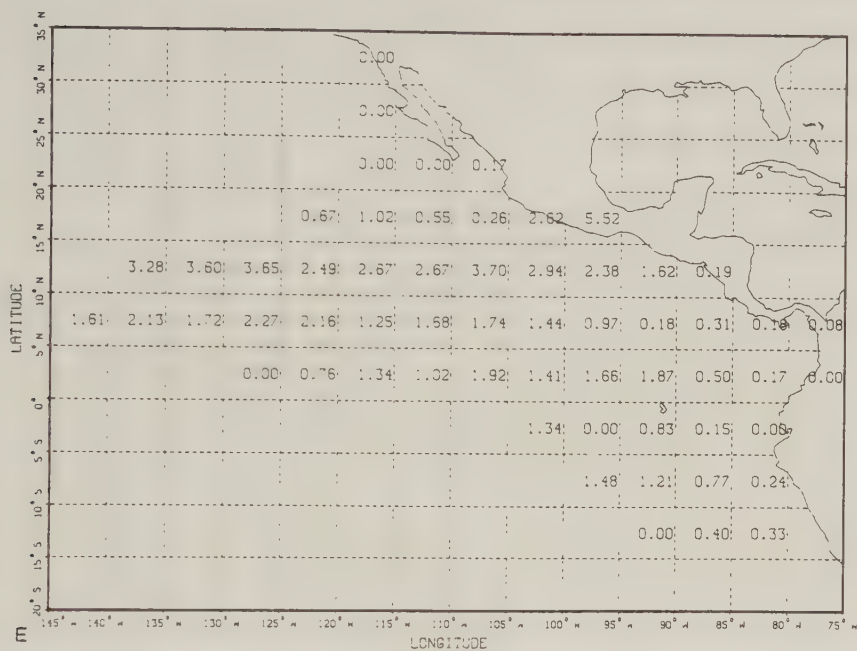


Figure 1. Continued. Weighted average estimates of the annual encounter rates (number of schools/1,000 mi searched) from 1977–1980 by 5° squares for marine mammal schools in the eastern tropical Pacific. (E) Mixed spotted and spinner schools. (F) Bottlenose dolphin schools.

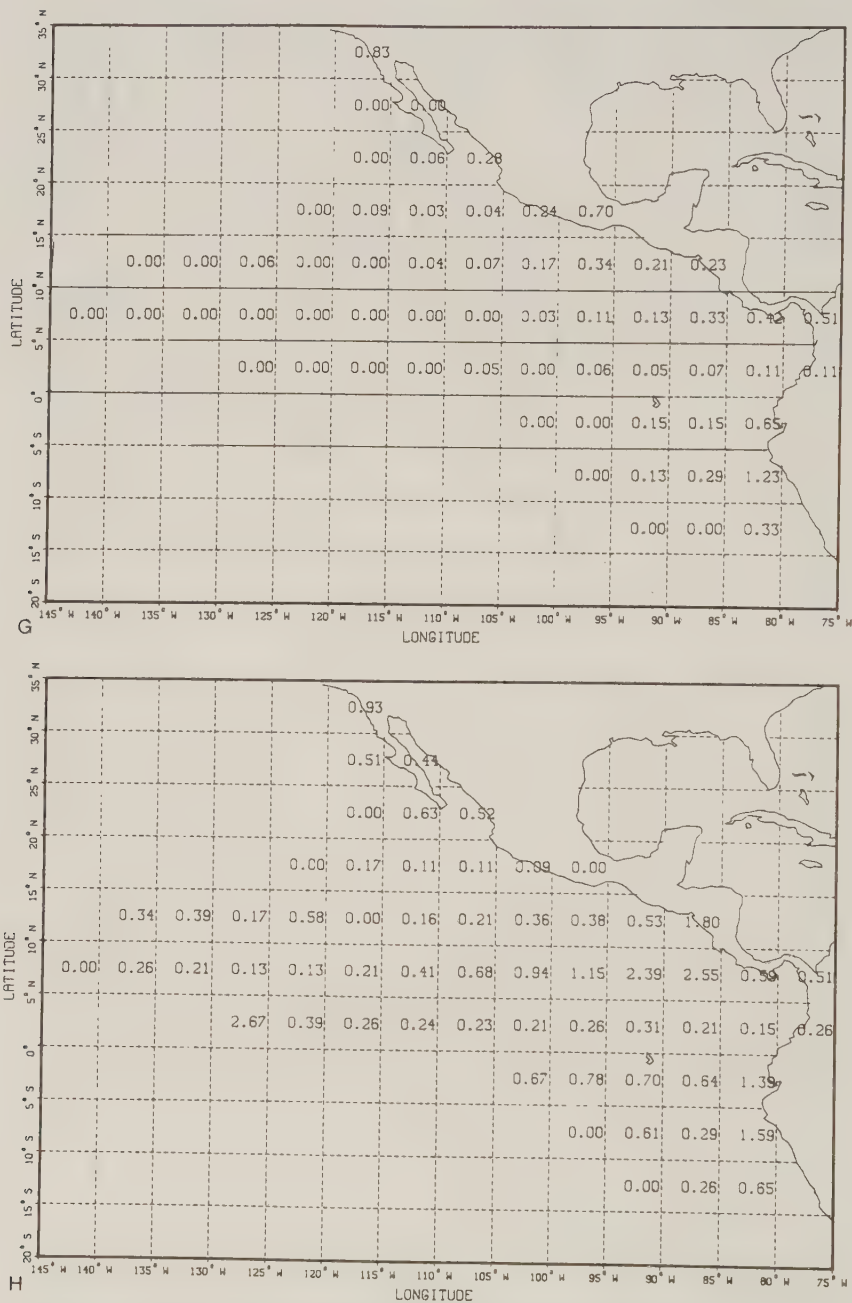


Figure 1. Continued. Weighted average estimates of the annual encounter rates (number of schools/1,000 mi searched) from 1977–1980 by 5° squares for marine mammal schools in the eastern tropical Pacific. (G) Risso's dolphin schools. (H) Pilot whale schools.

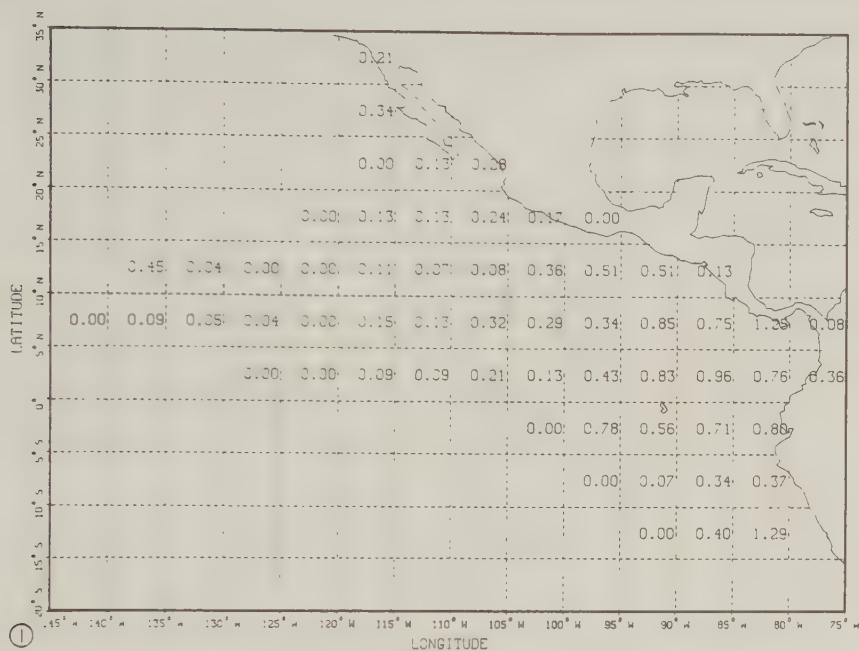


Figure 1. Continued. Weighted average estimates of the annual encounter rates (number of schools/1,000 mi searched) from 1977-1980 by 5° squares for marine mammal schools in the eastern tropical Pacific. (I) Sperm whale schools.

resulted in three factors with eigenvalues greater than 1.00. These three factors explain 63 percent of the variance in the original data.

Considering the factor loadings (Table 4), bottlenose dolphins, Risso's dolphins and pilot whales load strongly and are positively associated in the first factor. The common dolphin is also moderately associated with this first factor. The second factor is dominated by a positive association between spotted, spinner and mixed spotted and spinner schools. The common dolphin and to a lesser extent, the pilot whale are negatively associated with this factor. The third factor is dominated by the striped dolphin and sperm whales.

When separate factor analyses are performed on the data from each year, (1) the spotted, spinner and mixed spotted and spinner schools and (2) the bottlenose, common, Risso's and pilot whale schools tend to load together in the first few factors although there is some variability in this pattern, particularly in this latter grouping in 1980 (Table 5). Common dolphins also tend to be negatively associated with the factors associated with spinner and spotted dolphins. It is also interesting that, in 1978, schools of pure spinner dolphins appeared to be relatively independent of the distribution of either schools of mixed spotted and spinner or pure spotted dolphins.

The apparent association between sperm whales and striped dolphins suggested by the loading pattern for the third factor in the combined analysis may be spurious, given the factor loading patterns in the annual analyses, particularly

Table 3. Estimates of the correlation coefficients between nine types of cetacean schools based on the encounter rates in 5° squares from the combined data set for 1977-1980.

	Spotted dolphin	Spinner dolphin	Common dolphin	Striped dolphin	Mixed spotted/spinner	Bottle-nose dolphin	Risso's dolphin	Pilot whale	Sperm whale
Spotted dolphin	1.000								
Spinner dolphin	0.326	1.000							
Common dolphin	-0.325	-0.065	1.000						
Striped dolphin	-0.164	0.009	0.116	1.000					
Mixed spotted/spinner	0.478	0.370	-0.300	-0.173	1.000				
Bottlenose dolphin	0.054	0.240	0.307	0.029	0.061	1.000			
Risso's dolphin	-0.059	0.210	0.192	0.010	0.039	0.676	1.000		
Pilot whale	-0.188	-0.088	0.447	0.039	-0.221	0.551	0.389	1.000	
Sperm whale	-0.188	-0.152	0.273	0.197	-0.227	0.031	0.133	0.159	1.000

Table 4. The factor loading for the nine types of cetacean schools from the factor analysis on the combined set of encounter rate estimates by 5° square for 1977–1980. V.P. is the variance explained by a factor.

	Factor 1	Factor 2	Factor 3
Spotted dolphin	-0.092	0.712	-0.206
Spinner dolphin	0.209	0.743	0.140
Common dolphin	0.522	-0.430	0.237
Striped dolphin	-0.045	0.017	0.873
Mixed spotted/spinner	-0.046	0.755	-0.212
Bottlenose dolphin	0.885	0.188	0.008
Risso's dolphin	0.795	0.167	0.069
Pilot whale	0.760	-0.313	-0.017
Sperm whale	0.139	-0.271	0.580
V.P.	2.341	2.049	1.267

in light of the strong negative association between these two species in the third factor for 1977. However, these two species are known to be common in equatorial waters. Thus, the factor analysis may be picking out a true relationship and the reason the relationship does not appear stronger may be due to the fact that purse-seiners spend little time within the equatorial waters of the eastern tropical Pacific.

For the first factor from the combined analysis, there is a strong correlation between the factor scores for a 5° square in different years (Table 6). The annual factor score for a 5° square is a measure of the importance of the group of species that is strongly associated with a factor. The factor score is calculated as the sum of the products of the annual encounter rates for a 5° square for each species times its respective factor loading. A definite spatial pattern exists in these factor scores as can be seen in the tabulation of the annual score for each 5° square (Fig. 2A). Given the pattern in these factor scores, the positive factor loading for this first factor appears to represent a nearshore association of small cetaceans.

For the second factor from the combined analysis, the factor scores for a 5° square in different years also tend to be correlated (Table 6). A definite spatial pattern also exists for these factor scores (Fig. 2B). The positive values yield a pattern roughly similar to the pattern of relative density suggested by the detailed analysis of the encounter rate for spotted dolphins in Polacheck (1983). The areas with large negative values represent areas in which common dolphins and/or pilot whales are common and which lack schools of spotted and spinner dolphins.

Environmental Correlates

For almost all of the species, the maximum value of the estimated correlation coefficient between the encounter rates and any of the environmental variables has an absolute value between 0.30 and 0.45. The environmental variables

Table 5. The factor loading for the types of cetacean schools from the factor analyses on the annual encounter rate estimates by 5° squares. V.P. is the variance explained by a factor.

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 1	Factor 2	Factor 3
	1977				1979		
Spotted dolphin	0.805	-0.096	0.122		0.562	-0.323	-0.254
Spinner dolphin	0.730	0.289	-0.108		0.739	-0.145	0.153
Common dolphin	-0.616	0.402	0.151		-0.278	0.703	0.195
Striped dolphin	-0.320	-0.160	-0.671		-0.530	-0.152	0.666
Mixed spotted/spinner	0.819	0.088	0.058		0.795	-0.256	-0.085
Bottlenose dolphin	0.093	0.952	0.007		-0.025	0.200	0.847
Risso's dolphin	0.226	0.887	0.009		0.137	0.385	0.680
Pilot whale	-0.426	0.747	0.030		-0.083	0.800	0.187
Sperm whale	-0.249	-0.101	0.776		-0.413	0.669	0.030
V.P.	2.635	2.548	1.106		2.050	1.984	1.792
	1978				1980		
Spotted dolphin	0.005	0.839	0.013	0.095	0.713	-0.341	-0.153
Spinner dolphin	-0.024	0.145	0.041	0.873	0.764	0.253	-0.152
Common dolphin	0.580	-0.480	0.154	0.191	0.030	0.914	0.042
Striped dolphin	0.011	-0.084	0.806	0.256	0.388	0.174	0.564
Mixed spotted/spinner	-0.052	0.809	-0.196	0.167	0.548	-0.454	-0.135
Bottlenose dolphin	0.886	0.161	0.069	-0.004	0.663	0.167	0.292
Risso's dolphin	0.516	-0.454	-0.115	0.255	-0.123	0.013	0.797
Pilot whale	0.691	-0.105	0.198	-0.192	0.066	0.735	0.232
Sperm whale	0.230	-0.058	0.715	-0.220	-0.134	0.220	0.837
V.P.	1.922	1.862	1.282	1.052	2.021	1.868	1.860

Table 6. Estimates of the correlation coefficient between years for the first and second factor scores for a 5° square from the combined factor analysis. The lower triangle is for the first factor and the upper for the second. (n = the number of 5° squares.)

	1977	1978	1979	1980
1977		0.65 $n = 49$	0.50 $n = 48$	0.52 $n = 44$
1978	0.68 $n = 49$		0.61 $n = 49$	0.36 $n = 44$
1979	0.37 $n = 48$	0.68 $n = 49$		0.74 $n = 43$
1980	0.48 $n = 44$	0.68 $n = 44$	0.80 $n = 43$	

that tend to show the highest correlations tend to be associated with sea surface temperature, depth of the thermocline, thickness of the oxygen minimum layer and depth. Where the correlation with depth is relatively high, it is primarily a reflection of the nearshore distribution for these species.

The results from the regression analyses of the encounter rates on the principal components of the environmental variables yielded a highly significant relationship (Table 7). For all species, the first three components entering the analysis are generally significant at least at the 0.01 level. However, the cumulative R^2 for the regression coefficients never exceeds 0.40 for the first four components. This indicates that a large component of the variance in these encounter rates is not explained by these environmental variables. The principal component that most frequently enters early into the regression equations is number 2 (7 of 9). This component is dominated by variables related to sea surface temperatures, the thermocline, solar radiation and the variance in the depth of the oxygen minimum layer. Species that tended to be associated in the factor analysis tend to have similar principal components playing dominant roles in their regression equations.

Although the first principal component for the environmental data explains approximately 36 percent of the variation in the environmental data, it enters as one of the first four variables in only one of the regression equations. Also, many of the higher principal components are important in the regression equations. This suggests that a major part of the variation in cetacean densities is unrelated to the variation in these physical environmental parameters.

Canonical Correlations

The first few canonical correlation coefficients between the set of encounter rates for all species and the set of environmental variables tend to be surprisingly high and highly significant (Table 8) according to Bartlett's test for the significance of the smallest set of eigenvalues (Dixon 1981). The first canonical variable for the species variables has relatively high loadings or correlations with the encounter rates for all species. Schools of spotted, spinner and mixed spotted

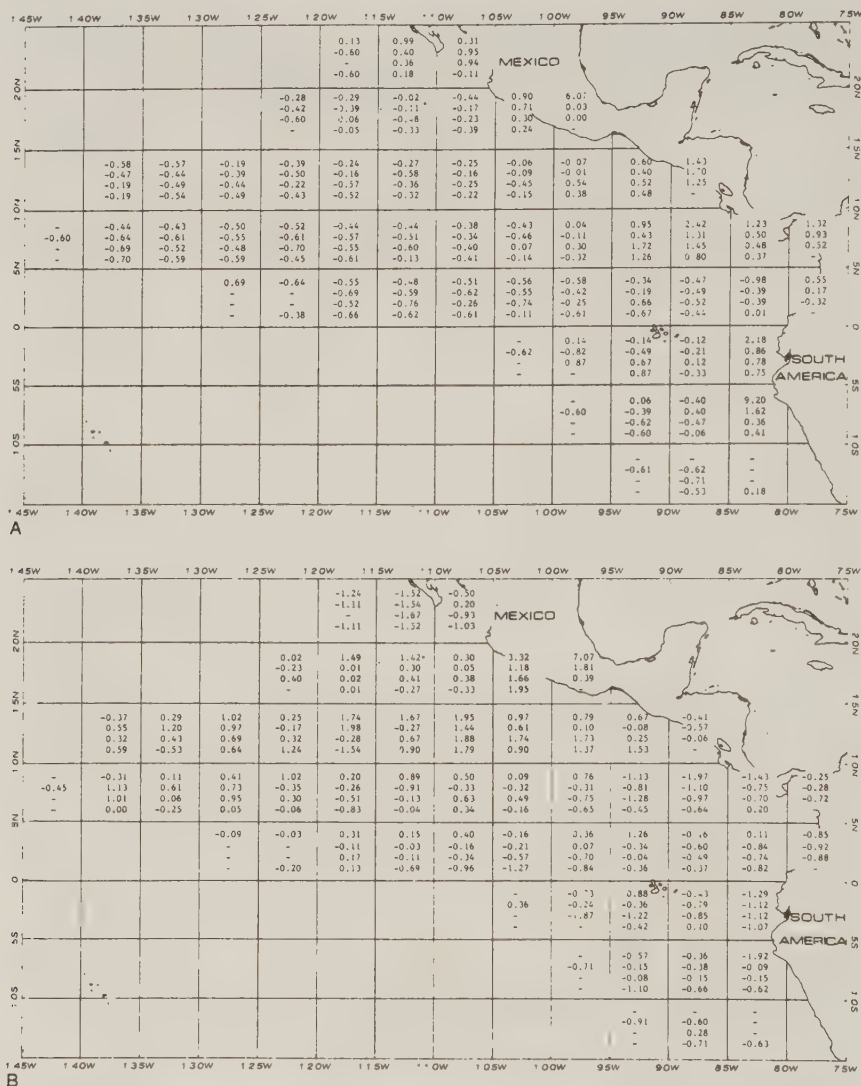


Figure 2. Estimates of the first (A) and second (B) factor scores for each year from 1977-1980 for a 5° square from the factor analysis on the combined data. The first value in a square represents the score for 1977, the second for 1978, etc. A dash indicates insufficient searching (*i.e.*, <500 mi) within a square during a given year.

and spinner schools load positively and the other six species load negatively. Thermocline depth, sea surface temperature and depth load most heavily in the first canonical variable for the set of environmental parameters (*see* Polacheck 1983 for complete listing of the loading). In general, the results of this canonical correlation analysis suggest similar results to the factor analysis and regression

Table 7. Results of the regression analyses of the encounter rates for nine types of cetacean schools on the principal components of the 13 environmental variables. Results

	First component to enter				Second component to enter		
	Com- po- nent num- ber	Corre- lation with en- counter rate	R ²	F-value to enter	Com- po- nent num- ber	Corre- lation with en- counter rate	R ²
Spotted dolphin	11	0.41	0.17	40.39***	2	-0.34	0.28
Spinner dolphin	4	-0.37	0.14	31.55***	2	-0.27	0.21
Common dolphin	6	0.38	0.15	34.41***	5	0.21	0.19
Striped dolphin	10	0.19	0.04	7.47**	2	0.18	0.07
Mixed spotted/spinner	2	-0.38	0.14	33.25***	6	-0.29	0.23
Bottlenose dolphin	3	-0.42	0.18	43.64***	4	-0.34	0.29
Risso's dolphin	5	0.40	0.16	36.82***	2	0.21	0.20
Pilot whale	5	0.33	0.11	24.76***	8	-0.27	0.19
Sperm whale	2	0.34	0.12	26.05***	3	-0.29	0.20

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.005$.

on principal components, but emphasize the extent of the large amount of overall inter-relation between the set of environmental variables and the encounter rates.

DISCUSSION

The above results indicate that the eastern tropical Pacific cannot be considered as a homogeneous community with respect to the common cetacean species found within it. The results of the factor analyses and estimates of the correlations between species suggest the existence of three major groupings in the spatial distributions of these species:

1. a nearshore grouping of bottlenose dolphins, Risso's dolphins, pilot whales and, to a lesser extent, common dolphins concentrated near the Gulf of Panama,
2. an offshore pelagic grouping of spotted and spinner dolphins, and
3. an association between pilot whales and common dolphins that overlaps the first grouping in nearshore areas and also tends to be segregated from the second grouping.

Striped dolphins and sperm whales have distributions overlapping all of these groupings and appear to have no strong association with any of the other species. The consistency of these major groupings both spatially and between years is surprising in view of the uncertainties and variability in estimates of relative

are given for the first four components to enter the regression equations for each school type.

F-value to enter	Third component to enter			F-value to enter	Fourth component to enter			F-value to enter
	Com- po- nent num- ber	Corre- lation with en- counter rate	R ²		Com- po- nent num- ber	Corre- lation with en- counter rate	R ²	
31.42***	6	-0.25	0.34	18.28***	8	-0.19	0.38	12.00***
18.46***	6	-0.18	0.24	8.73***	11	0.16	0.27	7.06**
11.14***	7	0.21	0.23	11.03***	2	0.16	0.26	6.49*
6.71*	3	-0.17	0.10	6.50*	8	0.10	0.11	1.99
21.18***	1	0.18	0.26	9.00***	4	-0.18	0.29	8.88***
31.38***	5	0.24	0.35	17.59***	8	-0.19	0.39	11.04***
11.24***	3	-0.17	0.23	7.45**	4	-0.15	0.25	5.84*
18.17***	3	-0.19	0.22	8.94***	9	0.17	0.25	7.74**
20.73***	5	0.21	0.24	11.01***	9	0.11	0.26	3.42

densities. This consistency is what most strongly suggests that these statistical groupings may reflect actual associations. However, these groupings should be considered primarily as hypotheses for further exploration because of the coarseness of both the geographic and temporal stratifications. The variation between years indicates that there is flexibility in whatever associations do exist.

Of these three species groupings, the association between spotted and spinner dolphins has been noted previously (Au *et al.* 1979). The fact that the observed correlation coefficients between these two species (Table 4) are not even larger is somewhat surprising given the frequency with which these two species are found together in a single school. The absence of higher correlations could reflect either the limits of the precision in the estimates and/or limits of the degree of actual overlap. The estimated range map (Holt and Powers 1982, Perrin *et al.* 1983) indicate the species do not overlap completely. Also, the association between spotted and spinner dolphins is probably less for the southern stocks, which would weaken the overall correlation since the highest encounter rates for pure schools of spinner dolphins are in the south.

Au *et al.* (1979) also suggest that striped and common dolphins may be closely associated in their distributions. There is not strong support for this association in the quantitative measures examined here, although the second highest correlation for the encounter rate of striped dolphins is with common dolphins (Table 3). The lack of any association could reflect simply the imprecision in the estimates of relative densities, particularly considering that striped dolphins are rarely sighted. This rarity of sightings is most likely due to the problem of unidentified schools discussed under MATERIALS AND METHODS (above).

Au *et al.* (1980) and Au and Pitman (1981) suggest that there is a unique

Table 8. Estimates of the canonical correlation coefficients and the eigenvalues from the canonical correlation analyses between the set of environmental variables and the set of encounter rate estimates. Also given are the results from Bartlett's test for the significance of the smallest set of eigenvalues. The results in the first row are for the test that none of the eigenvalues are different from 0. The results in the second row are for the test that all but the first eigenvalue are equal to 0, *etc.* The number of canonical variables of practical value is less than or equal to the smallest number of eigenvalues for which Bartlett's test for the remaining eigenvalues is nonsignificant.

Canonical variable pair number	Canonical correlation	Eigenvalue	Bartlett's test for the remaining eigenvalues		
			d.f.	Chi-square	P
—	—	—	117	584.9	0.0001
1	0.802	0.643	96	391.7	0.0001
2	0.710	0.505	77	259.8	0.0001
3	0.599	0.359	60	176.5	0.0001
4	0.517	0.267	45	118.2	0.0001
5	0.435	0.189	32	78.8	0.0001
6	0.426	0.181	21	41.3	0.0051
7	0.362	0.131	12	14.9	0.2459
8	0.253	0.064	5	1.5	0.7828
9	0.114	0.013	—	—	—

association of cetaceans with the equatorial surface water mass within the eastern tropical Pacific. This water mass tends not be frequented by purse seiners. Therefore, the results of this paper have no bearing on any such association.

As with the results from the factor analyses, the relationships suggested by the regression analyses between the spatial distribution of encounter rates and environmental parameters are surprisingly strong, but require even more caution in attributing any form of casual association, particularly since both the seasonal and annual variability is ignored in the set of environmental variables. However, even in spite of the uncertainties in both sets of data, the high canonical correlations and the R^2 s from the regression analyses suggest that a strong interdependence exists between the density of these cetacean schools and the environmental variation within the eastern tropical Pacific. These marine mammal species appear to have well-defined habits within the eastern tropical Pacific, determined in part by the physical environment. At the very least, the strong statistical relationships between these two sets of variables argue that the spatial patterns observed in the encounter rate estimates are unlikely to have arisen merely from sampling error, but reflect underlying patterns in the spatial densities of schools.

From the analyses of the relationship between these two sets of variables, parameters related to sea surface temperature, depth of the thermocline and thickness of the oxygen minimum layer tend to be the most important. These environmental parameters have been noted to correlate with the distributional ranges for the major dolphin species (Perrin *et al.* 1976, Au *et al.* 1979) and have also been noted to be related to tuna distributions (Blackburn 1965, Cole

1980, Forsbergh 1980, Sund *et al.* 1981). The significance, if any, of the thickness of the oxygen minimum layer is obscure.

The seven species other than the sperm whale considered in this paper are potentially major competitors. The available natural history information suggests that these seven species have overlapping diets, are opportunistic feeders on fish and squid in near-surface waters, have no significant predation pressure, are long-lived and have only limited capacities for rates of population growth (Leatherwood *et al.* 1972, Mitchell 1975; see also bibliographies of Johnson 1979, Rivers 1982). Traditional ecological theory on competition (*e.g.*, MacArthur 1968, May 1981) suggests that some form of resource partitioning must be occurring for these species to be co-occurring. The results from the factor and regression analyses are consistent with such partitioning. However, there is no direct evidence that any of these species are resource-limited. Even if this group has been structured by competition in the past, the large reduction in the abundances of spotted and spinner dolphins as the result of incidental kills during purse-seine operations (Smith 1979) suggests that the present should be a period of release from such competitive pressures. In this context, it would be interesting to examine changes in encounter rate estimates and in their spatial patterns if a longer time series of data becomes available.

ACKNOWLEDGMENTS

I wish to thank Dr. Peter Frank and Dr. Tim Smith for their generous support and useful comments during the research presented here. This paper would not exist without the data collected by the National Marine Fisheries Service observers. I wish to acknowledge these observers and the staff of the Southwest Fisheries Center of the National Marine Fisheries Service for collecting, editing and initially preparing these data. A number of the staff of the Southwest Fisheries Center provided support and technical assistance at various stages in this research. The number of people involved is too large to acknowledge each of them individually. Special thanks go to Phil Tarentino, Michael Lichter and Susan Boyer. Lily Tang, Ken Wallace, Veronica van Kouwen and the art department of the Southwest Fisheries Center were responsible for the final preparation of some of the figures. Veronica van Kouwen prepared the final typed manuscript. This report is a portion of a Ph.D. thesis submitted to the University of Oregon, Eugene, Oregon.

LITERATURE CITED

- AU, D. W. K., W. L. PERRYMAN AND W. F. PERRIN. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. National Marine Fisheries Service-Southwest Fisheries Center Admin. Report LJ-79-43. 59 pp.
- AU, D. W. K., W. L. PERRYMAN, R. L. PITMAN AND M. SINCLAIR. 1980. Cetacean populations and equatorial oceanography. Tropical Ocean-Atmosphere Newsletter 4:6, 10.
- AU, D. W. K., AND R. L. PITMAN. 1981. The equatorial cetacean community of the eastern Pacific. (Abstract.) Page 95 in Proceedings of Fourth Biennial Conference on the Biology of Marine Mammals, December 14-18, 1981. San Francisco, CA.
- BLACKBURN, M. 1965. Oceanography and the ecology of tunas. Oceanography and Marine Biology Annual Review 3:299-322.
- COLE, J. S. 1980. Synopsis of biological data on the yellowfin tuna, *Thunnus albacares* (Bonnaterre 1788), in the Pacific Ocean. Pages 71-150 in W. H. Bayliff, ed.

- Synopses of biological data on eight species of scombrids. Inter-American Tropical Tuna Commission Special Report No. 2.
- DIXON, W. J. (Ed.) 1981. BMDP Statistical Software. 1981 edition. University of California Press, Berkeley, CA. 726 pp.
- FORSBERGH, E. D. 1980. Synopsis of biological data on the skipjack tuna, *Katsuwonus pelamis* (Linnaeus 1758), in the Pacific Ocean. Pages 295-360 in W. H. Bayliff, ed. Synopses of biological data on eight species of scombrids. Inter-American Tropical Tuna Commission Special Report No. 2.
- HOLT, R. S., AND J. E. POWERS. 1982. Abundance estimation of dolphin stocks involved in the eastern tropical Pacific yellowfin tuna fishery determined from aerial and ship surveys to 1979. U.S. Department of Commerce, NOAA Technical Memorandum SWFC-TM-NMFS-23. 95 pp.
- JOHNSON, S. W. 1979. An annotated catalog of published and unpublished sources of data on populations, life history, and ecology of coastal marine mammals of California. National Marine Fisheries Service-Southwest Fisheries Center Admin. Report LJ-79-1. 193 pp.
- KENDALL, M. 1980. Multivariate analysis. MacMillan, New York, NY. 210 pp.
- LEATHERWOOD, S., W. E. EVANS AND D. W. RICE. 1972. The whales, dolphins and porpoises of the eastern North Pacific. A guide to their identification in the water. NUC-TP 282. 175 pp. Naval Undersea Research and Development Center, San Diego, CA 92132.
- LEATHERWOOD, S., W. F. PERRIN, V. L. KIRBY, C. L. HUBBS AND M. DAHLHEIM. 1980. Distribution and movements of Risso's dolphin, *Grampus griseus*, in the eastern North Pacific. Fishery Bulletin 77:951-963.
- MACARTHUR, R. H. 1968. The theory of the niche. Pages 157-176 in R. C. Lewontin, ed. Population biology and evolution. Syracuse University Press, Syracuse, NY.
- MAY, R. M. 1981. Models for two interacting populations. Pages 78-104 in R. M. May, ed. Theoretical ecology (2nd edition). Sinauer Associates, Sunderland, MA.
- MITCHELL, E. (Ed.) 1975. Review of biology and fisheries for smaller cetaceans: Report on the meeting of smaller cetaceans. Montreal, April 1-11, 1974. Journal of the Fisheries Research Board of Canada 32:889-983.
- PERRIN, W. F. 1968. The porpoise and the tuna. Sea Frontiers 14:166-174.
- PERRIN, W. F. 1969. Using porpoise to catch tuna. World Fishing 18:42-45.
- PERRIN, W. F. 1975. Distribution and differentiation of populations of dolphins of the genus *Stenella* in the eastern tropical Pacific. Journal of the Fisheries Research Board of Canada 32:1059-1067.
- PERRIN, W. F., J. M. COE AND J. R. ZWEIFEL. 1976. Growth and reproduction of spotted porpoise, *Stenella attenuata*, in the off-shore eastern tropical Pacific. Fishery Bulletin 74:229-269.
- PERRIN, W. F., G. J. SCOTT, J. WALKER, F. M. RALSTON AND D. W. K. AU. 1983. Distribution of four dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern tropical Pacific with an annotated catalog of data sources. U.S. Department of Commerce, NOAA Technical Memorandum SWFC-TM-NMFS-38. 65 pp.
- PERRIN, W. F., P. A. SLOAN AND J. R. HENDERSON. 1979. Taxonomic status of the "southwestern stock" of spinner dolphin *Stenella longirostris* and spotted dolphin *Stenella attenuata*. Report of the International Whaling Commission 29:175-184.
- PIELOU, E. C. 1977. Mathematical ecology. John Wiley and Sons, New York, NY. 385 pp.
- POLACHECK, T. 1983. The relative abundance of dolphins in the eastern tropical Pacific based on encounter rates with tune purse seiners. Ph.D. thesis, University of Oregon, Eugene, OR. 444 pp.
- POLACHECK, T. 1984. Documentation of the time sequential file created from the tuna boat observer data bases for analyzing the relative abundance of dolphins in the eastern tropical Pacific. National Marine Fisheries Service-Southwest Fisheries Center Admin. Report LJ-84-33. 26 pp.

- REILLY, S. B. 1977. The distribution of pilot whales, *Globicephala macrorhynchus* Gray 1846, in the eastern tropical Pacific. Master's thesis, California Polytechnic State University, San Luis Obispo, CA. 80 pp.
- RIVERS, V. 1982. Bibliography of marine mammal research programs at La Jolla Laboratory of Southwest Fisheries Center, 1963-1981. National Marine Fisheries Service-Southwest Fisheries Center Admin. Report LJ-82-25. 24 pp.
- SCHNELL, G. D., M. E. DOUGLAS AND D. J. HOUGH. 1982. Geographic variation in morphology of spotted and spinner dolphins (*Stenella attenuata* and *S. longirostris*) from the eastern tropical Pacific. National Marine Fisheries Service-Southwest Fisheries Center Admin. Report LJ-82-15C. 213 pp.
- SEBER, G. A. F. 1973. The estimation of animal abundance and related parameters. Griffin, London. 506 pp.
- SMITH, T. D. (Ed.) 1979. Report of the status of the porpoise stock workshop (August 27-31, 1979, La Jolla, California). National Marine Fisheries Service-Southwest Fisheries Center Admin. Report LJ-79-41. 120 pp.
- SUND, P. N., M. BLACKBURN AND F. WILLIAMS. 1981. Tunas and their environment in the Pacific Ocean: a review. Oceanography and Marine Biology Annual Review 19:443-512.

Received: July 9, 1985

Accepted: August 14, 1986

Assessment and Management of Deepwater Bottom Fishes in Hawaii and the Marianas

Jeffrey J. Polovina
Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
Honolulu, Hawaii 96822-2396

ABSTRACT

Stocks of deepwater snappers, groupers, and jacks in the Mariana Archipelago are just beginning to be exploited, and it is estimated from a 5-year fishery assessment program that the annual equilibrium yield for this resource will be 109 metric tons (MT). Stocks of deepwater bottom fishes in the Hawaiian Islands have a long history of exploitation and have been fished very heavily in recent years, especially around the populated islands. Commercial landings for 1984 are estimated at 414 MT from the populated islands and 662 MT for the entire archipelago. There is some evidence that the high fishing pressure at least around the populated islands has so substantially reduced the spawning stock biomass for at least one of the major species that the recent levels of yield may not be sustainable.

The Beverton and Holt yield equation is used to evaluate the impact of fishing mortality on spawning stock biomass, and some general guidelines are proposed: When the size of entry to the fishery exceeds the size of sexual maturity, fishing mortality should not exceed twice natural mortality; and when the size of entry to the fishery is less than or equal the size of sexual maturity, fishing mortality should not exceed natural mortality. The Beverton and Holt equation is also used to simulate multispecies interactions for a developing fishery that arise when fishing mortality applied to one species impacts another. As fishing mortality increases and concurrently the size of entry to the

fishery decreases, the catches of species with higher natural mortality to growth ratios will increase relative to those with lower natural mortality to growth ratios.

INTRODUCTION

The Hawaiian and Mariana Archipelagos support deepwater bottom fishes, which are a multispecies group consisting principally of snappers (Lutjanidae) and groupers (Serranidae), but also including jacks (Carangidae) in depths from 125 to 360 m. In Hawaii there is a long history of fishing for deepwater bottom fishes; currently the resource is fished throughout the archipelago and heavily fished around the populated islands (Ralston and Polovina 1982). In the Marianas the fishery for the deepwater bottom fishes is a much more recent development, and the stocks around many of the islands and banks are still unexploited. The first section of this chapter presents an estimate of the potential yield of the deepwater bottom fishes in the Marianas based on a recently concluded 5-year fishery assessment program by the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA. The next section treats the trends and estimated yield of the bottom fish fishery in the Hawaiian Islands, based primarily on a time series of commercial landings. The final section gives general guidelines on assessment and management of the deepwater bottom fishes for Pacific islands.

DEEPWATER BOTTOM FISH FISHERY IN THE MARIANAS AND ITS POTENTIAL YIELD

The Mariana Archipelago consists of a chain of islands and banks on a north-south axis, beginning with Galvez Banks and Santa Rosa Reef at the southernmost end and extending northward to Farallon de Pajaros, and a chain of seamounts also on a north-south axis about 120 nmi west of the high island chain (Figure 11.1).

The fishery for deepwater bottom fishes in the Marianas grew out of a program of exploratory fishing for deepwater snappers and groupers initiated in 1968 (Ikehara et al. 1970). The bottom fishing fleet consists of vessels 6 to 15 m long based primarily in Guam or Saipan. The vessels typically use electric or hydraulic gurdies



Figure 11.1 The Mariana Archipelago with the 22 islands and banks sampled

with a terminal rig consisting of a weight and four to six hooks, each attached to the mainline with a leader and spaced about a meter apart. From 1980 to 1984, the landings of deepwater bottom fishes in Guam have increased from 6 metric tons (MT) in 1980 to an estimated 20 MT in 1984. About 65 to 90% of the landings come from the waters around Guam.¹ The estimated commercial landings in Saipan for the period 1981 to 1984 ranged from 2 to 10 MT.¹

In 1980, a 5-year fishery assessment was begun in the Marianas, and the deepwater snappers, groupers, and jacks were one of the resource groups targeted. A total of 7,621 deepwater bottom fishes were caught with handline gear during six assessment cruises. Pristipomoides zonatus accounted for 51.2% of the catch and three species (P. zonatus, P. auricilla, and Etelis carbunculus) accounted for 79.1% of the total catch (Table 11.1).

The resource is relatively unexploited except around a few of the islands and banks where the collection of catch and effort data has recently been initiated. Thus, any approach to yield assessment must be independent of catch and effort data. In recent years, there have been a number of new methods and modifications of existing methods to estimate growth and mortality parameters, standing stock, and yield for fish stocks particularly in the absence of a time series of commercial catch and effort data (Beddington and Cooke 1983; Munro 1983a; Pauly 1983; Polovina 1986; Wetherall et al. In press). A number of these methods have been combined to produce an integrated approach to yield assessment that was applied to the multispecies resource of deepwater bottom fishes in the Marianas (Polovina and Ralston In press) (Figure 11.2). This approach to equilibrium yield estimation assumes: (1) that growth follows the deterministic von Bertalanffy curve with parameters K and L_{∞} ; (2) that the mortality of fish above the smallest length fully represented in the catch (L_c) occurs at a constant instantaneous rate (Z); (3) that recruitment is constant (R recruits entering the first age class annually); and (4) that the resource is essentially unexploited. Departures from some of these assumptions are discussed in Polovina and Ralston (In press).

The resource in the Marianas is essentially unexploited; thus an estimate for each species of the unexploited biomass that is recruited to the fishery and can be harvested with handline gear for each species was obtained from a systematic survey, and an estimate of

TABLE 11.1

List of species caught with bottom handline gear
in the Mariana Archipelago during the period
April 1982 to May 1984

Species	Number Caught	Percentage of Catch
Lutjanidae		
<u>Aphareus rutilans</u>	81	1.06
<u>Aprion virescens</u>	7	0.09
<u>Etelis coruscans</u>	202	2.65
<u>E. carbunculus</u>	952	12.49
<u>Pristipomoides sieboldii</u>	57	0.75
<u>P. filamentosus</u>	191	2.51
<u>P. auricilla</u>	1,170	15.35
<u>P. flavipinnis</u>	502	6.59
<u>P. zonatus</u>	3,904	51.23
<u>P. amoenus</u>	26	0.34
Carangidae		
<u>Seriola sp.</u>	60	0.79
<u>Carangoides orthogrammus</u>	9	0.12
<u>Caranx lugubris</u>	272	3.57
Serranidae		
<u>Serranidae sp.</u>	102	1.34
<u>Epinephelus morrhua</u>	15	0.20
<u>Cephalopholis iqarasihensis</u>	11	0.14
<u>Variola louti</u>	13	0.17
<u>Saloptia powelli</u>	47	0.62
Total	7,621	100

catchability was obtained from an intensive fishing experiment on a small isolated pinnacle (Polovina 1986). For each of the major species, an estimate of the von Bertalanffy growth parameter (K) was obtained from otolith data (Ralston and Williams Unpub.). Estimates of natural mortality (M) were obtained from large length-frequency samples by applying a regression model to the standard Beverton and Holt relationship for M/K in an unexploited stock, expressed as:

$$M/K = (L_{\infty} - \bar{l}) / (\bar{l} - L_c) \quad .$$

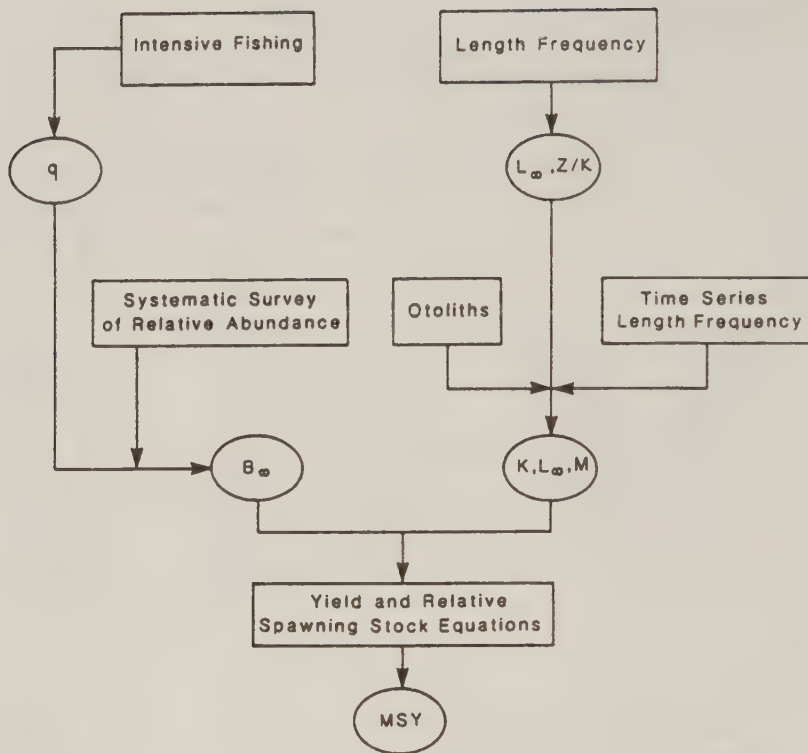


Figure 11.2 A schematic of the yield assessment approach--a more general approach to fishery assessment--which includes a treatment of catch and effort data as well is given in Munro (1983b); this figure represents a detailed subset of Munro's (1983b) figure 1

where L_c is the smallest length fully represented in the catch and $\bar{l}$ is the mean length of all fish greater than L_c (Beverton and Holt 1956). The regression approach constructs a series of L_c values at intervals beginning with the smallest L_c and going up to L_{∞} , together with the corresponding set of $\bar{l}$ values. By solving the M/K equation for $\bar{l}$ as a function of L_c , the following relationship is obtained:

$$\bar{l} = L_{\infty} / ((M/K) + 1) + L_c (M/K) / ((M/K) + 1) .$$

Thus, regressing a sequence of $\bar{l}$ values on the corresponding L_c values (with the appropriate weighting) produces

estimates for the slope and intercept that can be solved for L_∞ and M/K (Wetherall et al. In press).

The yield assessment approach is based on the Beverton and Holt yield equations, where equilibrium yield (Y) can be expressed as a function of growth (K), natural mortality (M), age of entry to the fishery (T_r), and fishing mortality (F) as:

$$Y = RF \int_{T_r}^{\infty} e^{(-tM - (t-T_r)F)} w(t) dt \quad ,$$

$$\text{with } w(t) = W(1 - e^{(-Kt)})^a \quad ,$$

where W is the asymptotic weight and a is the coefficient of allometry. The unexploited biomass recruited to the fishery (B_∞) can be expressed as:

$$B_\infty = R \int_{T_r}^{\infty} w(t) e^{(-tM)} dt \quad .$$

The ratio of equilibrium yield to unexploited recruited biomass (Y/B_∞) is independent of W and R and depends only on K , M , T_r , F , and a . Once an estimate of B_∞ is available, the equilibrium yield is estimated for a given level of fishing mortality as the product of Y/B_∞ and B_∞ .

Further, if the age of the onset of sexual maturity (T_m) is known, the spawning stock biomass (SSB) that corresponds to a given level of fishing mortality is:

$$SSB = R \int_{T_m}^{\infty} w(t) e^{-(t-T_r)F} e^{-tM} dt \quad \text{where } T_m \geq T_r$$

$$\text{and} \quad SSB = R \int_{T_m}^{T_r} w(t) e^{-tM} dt + R \int_{T_r}^{\infty} w(t) e^{-(t-T_r)F} e^{-tM} dt$$

$$\text{when } T_m < T_r \quad .$$

The ratio of the SSB for a specific level of F to the spawning stock biomass in the absence of exploitation (SSB_0) is a useful measure of the relative impact that F has on the SSB and under the assumption of constant recruitment is independent of R , depending only on T_m , K , T_r , M , F , and a .

In the systematic survey of the resource in the Marianas, seven species, one jack, Caranx lugubris, and six snappers, Pristipomoides zonatus, P. auricilla, P. filamentosus, P. flavipinnus, Etelis carbunculus, and E. coruscans, accounted for 92% of the catch (Table 11.1). Yield assessment was performed for each of these seven species plus an eighth group that consisted of all other species. For this latter group, the ratio (Y/B_∞) is estimated as the ratio of total yield for the seven species divided by their total unexploited recruited biomass. In this analysis, the age of entry for each species is the age that maximizes their yield per recruit.

The total equilibrium yield is computed as a function of F for the multispecies bottom fish complex fished with handline gear in the 125 to 275 m depth range for 22 islands and banks of the Mariana Archipelago. At each bank, the equilibrium yields are summed over the eight species groups to produce the bank equilibrium yield. The bank equilibrium yields then are summed over the 22 islands and banks surveyed. This archipelago yield increases rapidly as a function of fishing mortality to a

TABLE 11.2

Annual sustainable handline yield for the Marianas for the age at entry that maximizes the yield per recruit for each species in metric tons (MT)

Fishing Mortality (F)	Total Yield (MT)
0.1	35
0.5	91
1.0 ^a	109 ^a
1.5	114
2.0	116
2.5	116

^a $F_{0.1}$ and $Y_{0.1}$ as defined by Gulland (1983).

level of about 100 MT, exhibits only a gradual increase with increasing F (Table 11.2). The yield curve assumes constant recruitment; of course when F is sufficiently large, this assumption will no longer hold, the yield will decline. Ideally, a spawner-recruit relationship is needed to determine the sustainable yield curve. However, in the absence of that relationship, the maximum level of F that will be sustained before a serious reduction in recruitment occurs can be estimated from the ratio of spawning stock biomass under F relative to the unexploited spawning stock biomass. In the absence of any species-specific knowledge, it has been suggested that a substantial reduction in recruitment will occur if the spawning stock biomass of a species is reduced below 20% of its unexploited level (Beddington and Cooke 1983). With F of 1.0 and the age of entry that maximizes their yields per recruit, the spawning stock biomasses for the seven species are reduced to levels ranging from 20 to 42% of their unexploited levels, suggesting that recruitment will not be reduced significantly if the lower bound of 0.20

TABLE 11.3

The ratio of spawning stock biomass to unexploited spawning stock biomass as a function of F with the ages of entry for each species taken at the age that maximizes the yield per recruit^a

Species	Spawning Stock Biomass Relative to Its Level in the Absence of Exploitation		
	$F = 0.5$	$F = 1.0$	$F = 1.5$
<u>Caranx lugubris</u>	0.44	0.26	0.17
<u>Pristipomoides</u>			
<u>filamentosus</u>	0.46	0.33	0.28
<u>P. auricilla</u>	0.45	0.29	0.23
<u>P. flavipinnis</u>	0.45	0.26	0.17
<u>P. zonatus</u>	0.39	0.24	0.18
<u>Etelis coruscans</u>	0.31	0.20	0.15
<u>E. carbunculus</u>	0.58	0.42	0.34

^aBased on length of maturity (L_m) estimated as $L_m = 0.576 L_{max}$ (Anonyme 1977 in Brouard and Grandperrin 1984).

suggested by Beddington and Cooke is valid for these species (Table 11.3). As an alternative approach, the maximum sustainable yield (MSY) from the Beverton and Holt yield equation can be taken as the yield corresponding to that level of fishing mortality where an increase of one unit of fishing mortality will increase the catch by .0.1 of the amount caught by the very first unit of fishing mortality (Gulland 1983, 1984). This fishing mortality and corresponding yield have been denoted as $F_{0.1}$ and $Y_{0.1}$, respectively. The value of $F_{0.1}$ for the bottom fish resource in the Marianas based on this marginal yield approach is also estimated to be $F = 1.0$.

The annual equilibrium yield corresponding to $F = 1.0$ is 109 MT (an approximate 95% confidence interval is 81 to 137 MT (Polovina and Ralston In press)). About 70% of this yield would come from the southern islands and banks that include Guam and Saipan, 27% would come from the northern islands and banks, and only 3% from the seamounts (Table 11.4). This yield estimate can be converted to a yield per unit of bottom fish habitat. It is difficult to compute an area measure for the steep-sloped Pacific islands, and since the bottom fishes are found along the steep dropoff zones centered around the 200-m isobath, the length of the 200-m contour around an island or bank has been used as an index of bottom fish habitat. The means of the annual sustainable yield per nautical mile of 200-m contour for the northern banks, southern banks, and western seamounts are 212.9, 228.5, and 264.4 kg, respectively; a ratio of total yield for the archipelago to the total length of the 200-m contour is 222.4 kg/nmi of 200-m contour (95% confidence interval of 165.3 to 279.6 kg/nmi 200-m contour) (Table 11.4; Polovina and Ralston In press). There is, however, detailed bathymetry data from Guguan Island, one of the Northern Mariana Islands, where it is estimated that 1 nmi of 200-m isobath corresponds to 0.23 nmi² of habitat in the 125 to 275 m depth range (Polovina and Roush 1982). Based on this correspondence the unit MSY of 222.4 kg/nmi of 200-m contour for the Marianas is equivalent to approximately 1.0 MT/nmi² or 0.3 MT/km², which is at the lower end of the sustainable yield estimates for the bottom fish resources of the northwest Australian shelf (Sainsbury 1986).

There are two approximations to estimate MSY that express it as a fraction of the unexploited recruited biomass. Gulland (1969) uses a formula that estimates MSY as $0.5 MB_{\infty}$, where M is the instantaneous natural mortality and B_{∞} the unexploited biomass, and while Pauly (1983)

TABLE 11.4

Annual sustainable yield and yield per nautical mile of 200-m contour for the age at entry that maximizes the yield per recruit at a level of fishing mortality of $F = 1.0$ (MT = metric tons)

Location	Total Yield (MT/Year)	Yield (kg/year)/nmi of 200-m Contour
Northern Islands and Banks		
Maug	2.7	262.2
Asuncion	2.1	188.4
Agrihan	5.6	303.6
Pagan	7.7	255.1
Alamagan	2.0	177.6
Guguan	1.7	179.0
Sarigan	1.6	193.8
Anatahan	2.5	144.2
38-Fathom	0.5	187.3
Esmeralda	2.9	237.4
Total	29.3	Mean 212.9
Southern Islands and Banks		
Farallon de Medinilla	16.7	216.6
Saipan	13.4	254.1
Tinian	8.8	303.9
Aguijan	4.2	266.7
Rota	6.1	192.2
Guam	17.2	201.6
Galvez and Santa Rosa	8.6	164.2
Total	76.0	Mean 228.5
Seamounts		
Bank C	0.9	288.2
Bank D	1.1	351.2
Pathfinder	0.9	303.5
Arakane	0.6	199.6
Bank A	0.6	179.7
Total	4.1	Mean 264.4
Total yield from all banks	109 MT/year	

estimates MSY as $(2.3w^{-0.26}) B_{\infty}$, where w is the mean of the weight at sexual maturity and the asymptotic weight. A comparison of both these approaches with the values of Y/B_{∞} produced with the Beverton and Holt equation for the seven species shows that in four out of the seven the Y/B_{∞} values estimated with the Beverton and Holt equation lie between the values obtained from the Pauly and Gulland approximations. For the other three species, the Y/B_{∞} values fall slightly below the Pauly and Gulland estimates for two and substantially above for the third (Table 11.5). Thus, for at least six out of the seven species, the mean of the two estimates provides a useful approximation of Y/B_{∞} computed from the Beverton and Holt equation. Further, the means of these estimates for Y/B_{∞} are all in very close agreement.

Based on the estimate of catchability derived from the intensive fishing experiment, which represents lower bound for a commercial vessel, a fleet of 15 small vessels with two hydraulic or electric gurdies fishing 12 h a day, 200 days per year can produce the fishing effort approximately equal to the optimum fishing mortality of $F = 1.0$. The catch rate for this fleet would be about 1.5 kg per line-hour, and the average annual landing per vessel would be 7.3 MT.

TABLE 11.5

Annual maximum sustainable yield as a fraction of unexploited recruited biomass at $F = 1.0$ together with $0.5M$ and $2.3w^{-0.26}$

Species Groups	Y/B_{∞}	$0.5M$	$2.3w^{-0.26}$
<u>Caranx lugubris</u>	0.261	0.335	0.252
<u>Pristipomoides</u>			
<u>filamentosus</u>	0.262	0.270	0.296
<u>P. auricilla</u>	0.306	0.325	0.403
<u>P. flavipinnis</u>	0.680	0.475	0.348
<u>P. zonatus</u>	0.280	0.270	0.363
<u>Etelis coruscans</u>	0.201	0.175	0.226
<u>E. carbunculus</u>	0.375	0.515	0.289
Mean	0.338	0.338	0.311

DEEPWATER BOTTOM FISH FISHERY IN HAWAII AND ITS POTENTIAL YIELD

The Hawaiian Archipelago stretches from the Island of Hawaii to Hancock Seamounts 1,500 nmi to the northwest. The populated islands in the southern portion of the chain are often referred to as the main Hawaiian Islands, and the small, uninhabited islands, atolls, and seamounts that begin north of Niihau and extend northwest to Kure Atoll and Hancock Seamounts are called the Northwestern Hawaiian Islands (NWHI) (Figure 11.3).

There are 13 species groups that are harvested with deep-sea handline gear by the fishery (Table 11.6). Opakapaka, P. filamentosus, is the single most important species by weight, and the other major species consist of ulua (Caranx and Carangoides spp.), kahala, Seriola dumerili, uku, Aprion virescens, and onaga, Etelis coruscans. In 1984 opakapaka constituted 23% of the catch, and together onaga, opakapaka, uku, and ulua accounted for almost 70% of the landings.

Unlike the situation in the Marianas, there is a long history of commercial fishing for deepwater bottom fish in the Hawaiian Islands. There was a fleet of vessels that fished the deepwater bottom fishes throughout most the archipelago at least as early as the 1930s. Catch records from 1945 to 1982 indicate that the commercial landings

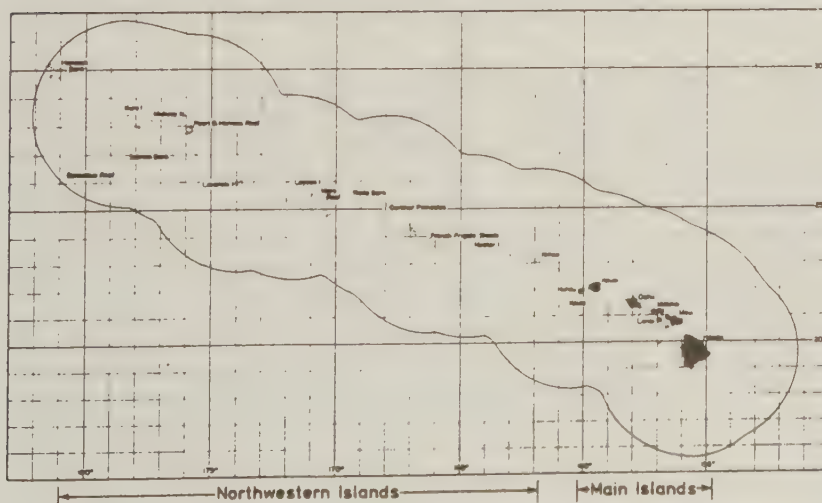


Figure 11.3 The Hawaiian Archipelago

TABLE 11.6
Principal species of fish landed in the Hawaiian
offshore handline fishery

Family	Species	Common Name	Range of Landed Weight (kg)
Lutjanidae	<u>Aphareus rutilans</u>	Lehi	3-8
	<u>Aprion virescens</u>	Uku	2-8
	<u>Etelis coruscans</u>	Onaga	2-8
	<u>E. carbunculus</u>	Ehu	0.5-2
	<u>Lutjanus kasmira</u>	Taape	0.5
	<u>Pristipomoides</u>		
	<u> filamentosus</u>	Opakapaka	1-6
	<u>P. sieboldii</u>	Kalekale	0.5
	<u>P. zonatus</u>	Gindai	0.5-2
Carangidae	<u>Caranx</u> and		
	<u>Carangoides</u> spp.	Ulua	1-10
	<u>Seriola dumerili</u>	Kahala	3-10
Serranidae	<u>Epinephelus guernus</u>	Hapuupuu	3-10
Labridae	<u>Bodianus</u> spp.	Aawa	1-3
Scorpaenidae	<u>Pontinus macrocephala</u>	Nohu	1-2

for the State began at about 450 MT after the hiatus imposed by World War II, declined rapidly to a level of about 180 MT by 1959, and remained relatively stable at around 180 MT until 1974, when landings began steadily increasing (Figure 11.4). These catch data come only from fishermen with commercial fishing licenses and do not include the catches from the recreational fishermen, which may be substantial around the populated islands. An estimate of the commercial landings for the State for 1984 is 662 MT, which indicates that commercial landings have continued their rapid increase and are now greater than at any time since World War II (Figure 11.4).² The high catches from 1948 to 1953 correspond to catches for a period when both the NWHI and main Hawaiian Islands were fished. However, from the mid-1950s until about 1975, when there was renewed interest in the stocks of the NWHI,

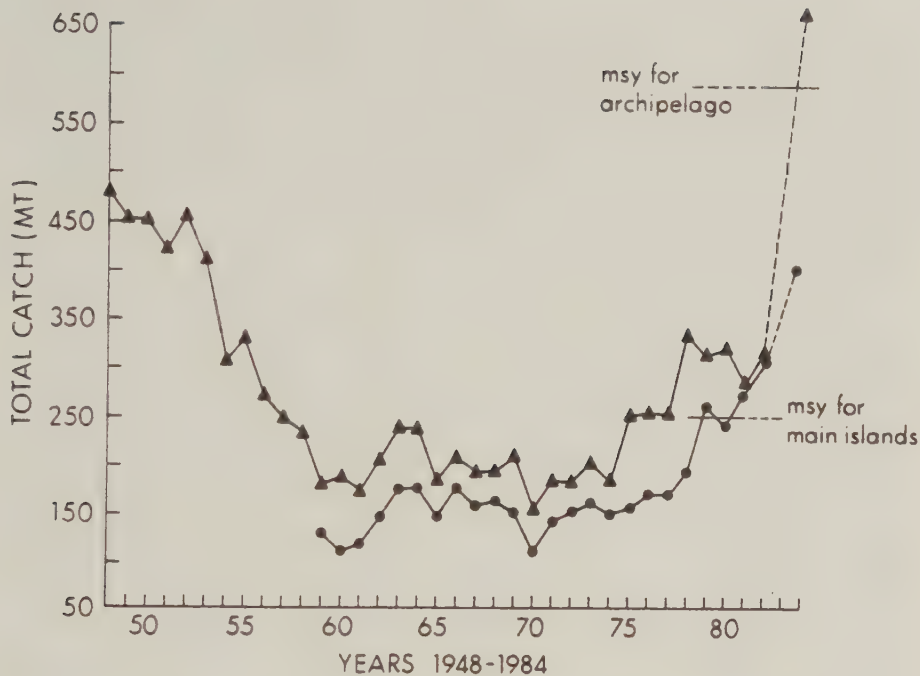


Figure 11.4 The annual commercial landings for deepwater bottom fishes from the main islands and the entire archipelago for 1948-1984. Data reported by State of Hawaii, Division of Aquatic Resources. $\blacktriangle$ = archipelago landings; $\bullet$ = main island landings

most of the fishing was restricted to the main Hawaiian Islands. Records of landings from the main Hawaiian Islands are available only since 1959. Landings have fluctuated in the range of 100 to 200 MT from 1959 to 1978 while since 1978 have shown rapid growth. The estimated catch for 1984 is 413.6 MT. The rapid increase in landings from the main Hawaiian Islands and from the entire State since 1978 is a direct result of an expansion of the local market for fresh bottom fishes at a relatively stable and strong price (Pooley 1986). In 1984 the wholesale prices for bottom fishes averaged \$5.83/kg, and onaga and opakapaka commanded the highest prices at \$8.80 and \$7.37/kg, respectively.²

The species composition of the commercial landings from the main islands does not show any radical changes from 1959 to 1984, but some of the species do exhibit

substantial relative increases or decreases (Table 11.7). Some of these changes are readily explainable, such as a decline of kahala (grouped in the Others category) due to its implication in ciguatera poisoning, the relative increase of onaga, the deepest water species, due to increasing fishing pressure in deeper habitat as the total fishing pressure increases, and the corresponding relative decline of the shallower water species ulua and uku due to overfishing in shallow waters.

The first approach to yield assessment for this multispecies fishery was fitting a Schaefer surplus production model to the commercial catch and effort data (measured in vessel days) for 1959-1978 (Ralston and Polovina 1982). For this analysis the main islands were grouped into four banks that are separated by deep channels and hence assumed to represent closed populations since adults and juveniles are not known to move across deep channels. The Islands of Oahu and Hawaii each formed their own bank; Kauai, Niihau, and Kaula Islands were pooled as one bank because of their proximity to each other; and the Islands of Maui, Lanai, Kahoolawe, and Molokai (MLKM) were treated as a single bank since the depths between them were <200 m. At first, single species surplus production models were applied to all 13 species for each of the 4 banks, but most of the fits were not

TABLE 11.7

Commercial landings of deepwater bottom fishes from the main Hawaiian Islands (in metric tons)

Species	1964	(%)	1974	(%)	1984	(%)
Ehu	9.3	(5.2)	9.4	(6.3)	16.7	(4.0)
Gindai	0.7	(0.4)	0.5	(0.3)	2.1	(0.5)
Hapuupuu	4.0	(2.3)	8.5	(5.7)	25.1	(6.1)
Kalekale	7.1	(4.0)	2.2	(1.5)	10.8	(2.6)
Lehi	0.4	(0.2)	1.9	(1.3)	7.4	(1.8)
Onaga	21.7	(12.2)	17.7	(11.8)	86.7	(21.0)
Opakapaka	42.4	(23.9)	48.7	(32.4)	96.2	(23.2)
Uku	40.1	(22.6)	35.0	(23.3)	66.4	(16.1)
Ulua	13.8	(7.8)	12.0	(8.0)	27.1	(6.6)
Others	38.0	(21.4)	14.1	(9.4)	75.0	(18.1)
Total	177.5		150.0		413.6	

statistically significant. The poor fit of the single species models was probably a result of using effort measured in vessel-days, because a vessel-day produces a multispecies catch; hence this represented a measure of multispecies effort more than effort directed toward any particular species. Next, 2 aggregated multispecies surplus production models were applied, 1 to the 13 species pooled together, the total biomass Schaefer model, and the other to 3 separate species groups formed by aggregating the species according to their depth distribution.

The MLKM bank, which accounts for over 50% of the State bottom fish landings, is the only bank where both approaches produced statistically significant results. The application of the Schaefer model to the three aggregated species groups explained only slightly more of the total variation in catch than the total biomass Schaefer model. As a first approximation, treating the 13 species bottom fish resource with the total biomass model is appealing. All the species occupy a very similar range of habitat, all the species appear to be high level carnivores with no evidence of prey-predator interactions among them, and fishing for one species also exerts pressure on other species.

The estimated MSY based on the total biomass Schaefer model for the MLKM bank is 106 MT, which corresponds to a unit MSY of 272 kg/nmi of 200-m contour (Ralston and Polovina 1982). This estimate is a lower bound since it includes only commercial landings and not the recreational catch, which could be substantial.

The lengths of the 200-m contour for the main islands and the NWHI are 977 and 1,231 nmi, respectively. Based on the annual MSY estimate of 272 kg/nmi of 200-m contour, the MSY is estimated at 266 MT for the main islands, 335 MT for the NWHI, and 601 MT for the entire archipelago. Since 1979 the landings from the main islands have exceeded the estimated MSY level, and the 1984 estimated landings of 414 MT were 55% above the MSY. Landings from the NWHI for 1984 were 74% of the MSY.

It is difficult to obtain an accurate measure of fishing mortality for the resource. Over the period 1959-1978, where a measure of effort in vessel-days is available, there was a threefold increase in vessel days (Ralston and Polovina 1982). However, technological changes such as electric or hydraulic gurdies, fathometers, chromoscopes, and loran have increased the fishing power of the vessel so that the trend in vessel days underestimates the real trend in fishing mortality. In

addition to the considerable increase in fishing mortality in recent years, there is evidence, at least for opakapaka in the main islands, of substantial decrease in the age of entry to the fishery between 1980 and 1984 (Ralston and Kawamoto 1985). A yield-per-recruit analysis indicates that in 1980 the age of entry and fishing mortality for opakapaka on Penguin Bank were 4 years and 0.48/year, respectively, which placed it on the eumetric line of the yield-per-recruit isoplath (Ralston 1984). By 1984, however, a weight-frequency distribution for fish landed from the main Hawaiian Islands indicated that the age of entry was 1.8 years, which, with a fishing mortality of 0.48/year, results in a 17% reduction from the 1980 yield-per-recruit level (Ralston and Kawamoto 1985). When the approach used in the Marianas analysis to compute the ratio of the exploited to unexploited spawning stock biomass is applied to opakapaka stocks in the Hawaiian Islands with an age of entry of 1.8 years and a fishing mortality of 0.5/year, it is estimated that the spawning stock biomass is reduced to 10% of its unexploited level. This compares with 28% of its unexploited level when the age of entry is 4 years and the level of fishing mortality remains the same.

MANAGEMENT IMPLICATIONS

If the range of annual sustainable yield of 165 to 280 kg/nmi of 200-m contour estimated in the Marianas is taken as an archipelago range for Pacific islands and applied to the main Hawaiian Islands, an upper bound of sustainable yield is estimated at 274 MT annually. The landings from the main islands have exceeded this level since 1980, and by over 55% in 1984. This raises questions about the general nature of the range. However, given the evidence of growth overfishing, at least for opakapaka, and the reduction of its spawning stock biomass to as low as 10% of its unexploited level, it also suggests that these high levels of yield may not be sustainable.

Whereas the total biomass approach for multispecies bottom fish stocks is useful as a first step for assessment and management, it can be refined with a species specific approach based on the Beverton and Holt yield equation. This equation, appropriately formulated, requires only estimates of Z/K , F/M , L_C/L_∞ , and L_∞/L_∞ for yield-per-recruit and relative spawning stock analyses

(Beverton and Holt 1966; Beddington and Cooke 1983). Given that some of the recent length-based methods produce efficient estimators of Z/K when applied to large length-frequency samples, it is possible to develop species specific management of deepwater bottom fishes for Pacific islands based only on length-frequency samples. Even heavily fished archipelagos such as Hawaii have relatively unfished areas that can be sampled to estimate M/K . Fished banks will provide an estimate of Z/K that, together with M/K , provides an estimate of F/M . These estimates, together with estimates of L_c/L_∞ and L_m/L_∞ , which are also easy to obtain from length-frequency samples and maturation studies, can be used to determine if the stock departs from the eumetric line and to estimate relative spawning stock biomass. Further, a time series of species specific estimates of Z or even Z/K obtained from length-frequency data, together with total catch data, can be used as the basis for single species production modelling (Csirke and Caddy 1983).

Based on the Beverton and Holt yield equation, upper bounds on F relative to M can be established as a function of L_c/L_∞ . Consider the bottom fishes that have M/K values falling within the range of 1.0 to 4.0, which appears to include a large number of the snappers and groupers (Munro 1983b; Bannerot 1984; Ralston 1986; Polovina and Ralston In press). Further, suppose that the size of the onset of sexual maturity is estimated as $L_m = 0.5 L_\infty$, which appears valid for most snappers (Grimes 1986). The ratio of spawning stock biomass under exploitation to the spawning stock biomass in the absence of fishing, computed as a function of F/M with the Beverton and Holt yield equation, is presented in Figure 11.5. Calculations were performed for two levels of M/K , 1.0 and 4.0, and for three levels of L_c/L_∞ , 0.4, 0.5, and 0.6. When M/K is 4.0 and L_c/L_∞ is 0.6, the stock can sustain high levels of exploitation with minimal impact on the spawning stock. This is because when M/K is high and harvesting occurs above the size of sexual maturity, most of the contribution to the spawning stock comes from fish between the sizes L_m and L_c . However, when harvesting occurs at or below L_m , or if harvesting is above L_m and M/K is low, there is an exponential decline in the relative spawning stock biomass as a function of F/M . If L_c is greater than L_m , it appears that the relative spawning stock biomass for a fixed level of exploitation (F/M) increases with increasing M/K . Conversely, when L_c is less than L_m , the greater M/K , the lower the relative spawning stock biomass. If it is

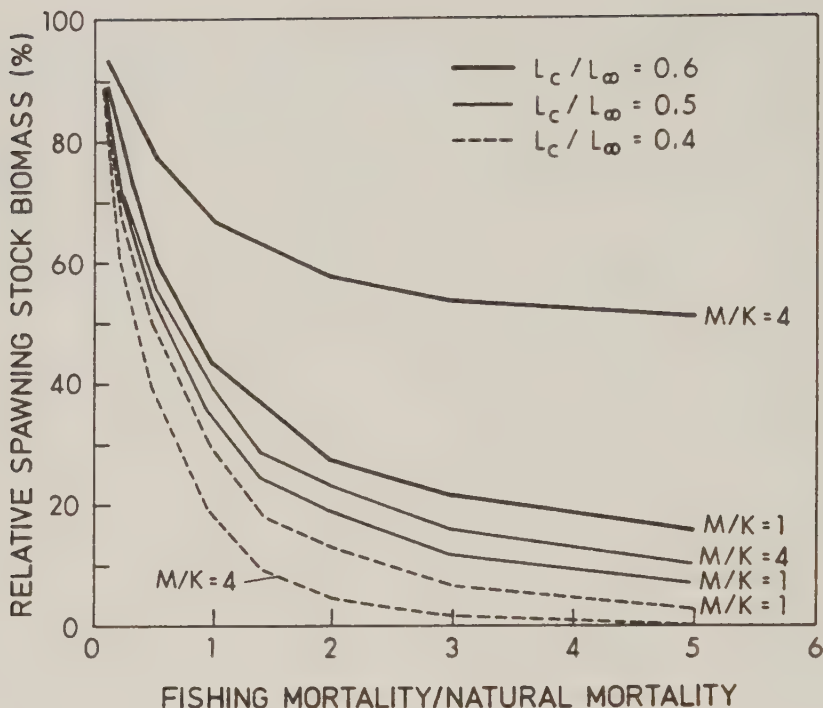


Figure 11.5 The ratio of spawning stock biomass as a function of fishing mortality to spawning stock biomass in the absence of exploitation for two levels of M/K and three levels of L_c/L_∞ when $L_m/L_\infty = 0.5$

determined that the exploited spawning stock biomass should not fall below about 20% of its unexploited level, then for fishes with M/K values in the range of 1 to 4 and when L_m is $0.5 L_\infty$, F should not exceed $2M$ if L_c is greater than or equal to L_m and F should not exceed M if L_c is below L_m .

Prey-predator interactions do not appear to be strong for the bottom fish community (Parrish 1986), and hence multispecies interactions are probably negligible (Ralston and Polovina 1982). However, multispecies interaction in the form of changes in relative species abundance may occur. For example, based on the Beverton and Holt equation it can be shown that in a multispecies fishery as F increases from a lightly exploited situation to a heavily exploited situation and concurrently the age of entry decreases, the yield per recruit of those stocks

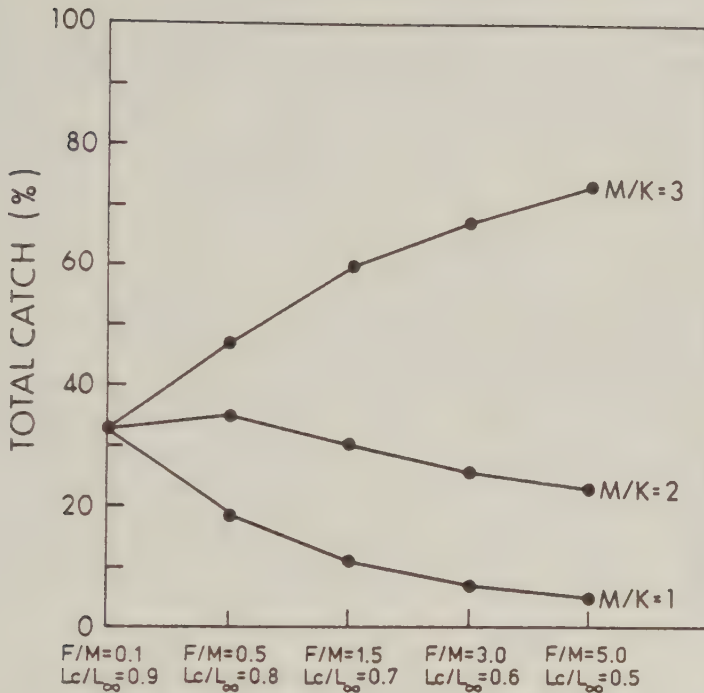


Figure 11.6 The relative contribution to the total catch for a multispecies group consisting of three species with different M/K values as a function of fishing mortality to natural mortality (F/M) and relative age of entry L_c/L_∞

with the higher M/K values will increase relative to the yield per recruit of those stocks with the lower M/K values. Simulation on a three-species group with M/K values of 1, 2, and 3, which represents a reasonable range for the bottom fishes in Hawaii, begins with F/M equal to 0.1, size of entry equal to 90% L_∞ , and each species accounting for one-third of the landings. When F/M has increased to 3 and size of entry to 60% L_∞ , (and assuming no change in recruitment for each species), the species with M/K of 3 will account for 67% of the landings while the species with M/K of 1 will only account for 7% (Figure 11.6). Further, the ratio of the exploited spawning stock biomass to unexploited spawning stock biomass will decline more rapidly for the species with low M/K values than for the species with higher M/K values (when L_c is greater than L_m), possibly adding further to the reduction of the

relative contribution of low M/K species (Figure 11.5). It is the change in the age of entry more than the change in fishing mortality that is responsible for the change in relative yield.

Once the age of entry has been reduced substantially below the optimum value based on yield per recruit and relative spawning stock biomass analysis, as it appears to be for opakapaka in the main Hawaiian Islands, management recommendations that increase the age of entry must be sensitive to the dynamic or short-term response of the fishery. Even though yield-per-recruit analysis indicates that the long-term equilibrium yield will be increased with an increased age of entry, the short-term loss may exceed the long-term gain to the fishermen while the population structure of the stock is readjusting to the higher age of entry (Huntsman and Waters 1986). In such situations, management may find that a gradual increase in the age of entry through small annual increments is preferable to a single step increase to the optimal age of entry.

Although the mean level of the exploited spawning stock biomass relative to the unexploited level has been used to determine the level of exploitation that can be sustained, the variation in spawning stock biomass about this mean level has not been considered. If variation in recruitment is substantial, it may induce variation in the spawning stock biomass, which may have a greater impact on the sustainability of a level of yield than the mean value of the spawning stock biomass (Beddington and Cooke 1983). If it is assumed that recruitment is random and annual values are independent and identically distributed about a mean R with a coefficient of variation (standard deviation divided by mean) of s , and if it is assumed that the year-to-year variance in growth and mortality are negligible, then variances for annual yield, spawning stock biomass, and recruited biomass can be derived by computing the variance of yield, spawning stock, or biomass for a cohort of age t and integrating that variance with respect to t (Beddington and Cooke 1983). For example, the variance of the recruited biomass ($V(B)$) in the absence of exploitation is:

$$V(B) = R^2 s^2 W^2 \int_{T_r}^{\infty} \exp(-2tM) (1 - \exp(-Kt))^6 dt$$

Beddington and Cooke (1983) provide an approximation based on the Beverton and Holt equation that expresses the coefficient of variation (c.o.v.) of either the catch, the recruited biomass, or the spawning biomass as the same function of the coefficient of variation of recruitment (s) and total mortality (Z) as:

$$\text{c.o.v.} = (2/3)s(Z)^{0.5} \quad (1)$$

Thus, if catch data are available for a period where Z is relatively constant and known, the c.o.v. of recruitment can be estimated, and the c.o.v. of the spawning stock biomass determined as a function of Z . With this latter relationship, confidence intervals of the relative spawning stock biomass can be computed as a function of F . In a number of instances it appears that annual recruitment and hence spawning stock biomass has a lognormal distribution, so the appropriate transformation must be applied to the variance of the spawning stock biomass before confidence intervals based on normal theory can be used.

This approach will be applied to estimate the lower bound of a 90% confidence interval of the relative spawning stock biomass for opakapaka when F is 0.5/year, age of entry to the fishery is 1.8 years, and age of sexual maturity is 3.25 years (the parameters that appear to represent the condition of the stock around the main islands in 1984 (Ralston and Kawamoto 1985)). The c.o.v. of the catch for the opakapaka fishery was estimated at 0.23 by using annual landings from just the main island catch for 1959 to 1970, when fishing effort was relatively constant. From Equation 1 with Z estimated to be 0.5 ($M = F = 0.25$) over the period 1959-1970 and the c.o.v. for opakapaka catch of 0.23, s is estimated to be 0.49. An estimate of the c.o.v. for opakapaka spawning stock biomass (SSB) is then estimated from Equation 1 as:

$$\text{c.o.v. (SSB)} = (0.49) (2/3) \sqrt{0.25 + F} .$$

When the mean spawning stock biomass is at 10% of the unexploited spawning stock biomass (SSB_0), which corresponds to $F = 0.5$, Equation 1 becomes:

$$\text{c.o.v. (SSB)} = 0.28$$

$$\begin{aligned}
 \text{or standard deviation (SSB)} &= 0.28 \text{ mean (SSB)} \\
 &= 0.28 (0.1)(\text{SSB}_0) \\
 &= 0.028 \text{ SSB}_0 .
 \end{aligned}$$

$$\text{Thus, variance } \left(\frac{\text{SSB}}{\text{SSB}_0} \right) = 7.84 \times 10^{-4} .$$

A confidence interval for the relative spawning stock biomass can be obtained by transforming the lognormally distributed spawning stock biomass into a normally distributed variable. When the mean value for the spawning stock biomass is 10% of its unexploited value, the lower bound of the 90% confidence interval is 6% of its unexploited level. Thus, when recruitment variation is not considered, it is estimated that the spawning stock biomass of opakapaka around the main islands in 1984 was at about 10% of its unexploited level, but when variation in recruitment is taken into account, the relative spawning stock biomass could have been as low as 6%. It is interesting that the c.o.v. of recruitment for opakapaka estimated at 0.49 is slightly less than most of the estimates of the c.o.v. of recruitment for 18 temperate species that typically exceeded 0.6 (Hennemuth et al. 1980).

Beyond the conventional management approaches such as regulating the age of entry to the fishery and the fishing pressure, fishery enhancement may provide opportunities to increase yields of deepwater bottom fishes around Pacific islands. One approach to fishery enhancement in Hawaii has been the introduction of species groups that were underrepresented among the native fauna of the Hawaiian Islands, with the idea that these groups would fill a niche in the ecosystem and add to the total fishery yield. Between 1955 and 1961, 11 species of Serranidae, Lutjanidae, and Lethrinidae were introduced. Only three species have established significant populations: the grouper, Cephalopholis argus, and a snapper, Lutjanus fulvus, which only constitute a minor component of the commercial landings, and taape, Lutjanus kasmira, which has spread widely throughout the archipelago. The commercial catch of taape is 30 MT, and most probably would be considerably greater if market prices were higher (Oda and Parrish 1981). Although the introduction of taape appears to have increased the total yield of the bottom fish fishery and there does not appear to be a major dietary overlap

between taape and any native species, some fishermen complain that it competes aggressively and successfully for fishing gear so that catches of more desirable native species are reduced (Oda and Parrish 1981).

Artificial reefs represent another fishery enhancement approach that may increase the production of deepwater bottom fishes. In Hawaii, many banks that support populations of snappers and groupers along their perimeters have flat, sandy tops in the 50 to 90 m depth range that support very low densities of fish. If the low densities of fish over the tops of these banks are a result of the lack of suitable habitat, and recruitment is not limiting, artificial reefs placed on these banks can offer appropriate habitat to support an increased standing stock and hence a yield of commercially valuable bottom fishes. The total area of habitat utilized by deepwater snappers and groupers in the Hawaiian Archipelago is about 2,000 nmi². Penguin Bank alone offers an area of 500 nmi² of level, sandy habitat which currently supports only a very low density of commercially valuable fishes. If appropriate habitat is a limiting factor, artificial reefs placed on Penguin Bank alone can increase the productive bottom fish habitat in the State by 25%.

NOTES :

1. Data on file with Western Pacific Fishery Information Network, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396.

2. Data from Western Pacific Regional Fishery Management Council.

BIBLIOGRAPHY

- Bannerot, S. P. 1984. The dynamics of exploited groupers (Serranidae): An investigation of the protogynous hermaphroditic reproductive strategy. Ph.D Dissertation, Univ. Miami, Coral Gables, 393 p.
- Beddington, J. R., and J. G. Cooke. 1983. The potential yield of fish stocks. FAO Fish. Tech. Pap. 242, 47 p.
- Beverton, R. J., and S. J. Holt. 1956. A review of methods for estimating mortality rates in fish populations, with special reference to sources or

- bias in catch sampling. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 140:67-83.
- _____. 1966. Manual of methods for fish stock assessment. Part 2. Tables of yield functions. FAO Fish. Tech. Pap. 38, Rev. 1, 67 p.
- Brouard, F., and R. Grandperrin. 1984. Les poissons profonds de la pente recificale externe a Vanuatu. Mission ORSTOM, Vanuatu, Notes Doc. Oceanogr. 11, 131 p.
- Csirke, J., and J. F. Caddy. 1983. Production modeling using mortality estimate. Can. J. Fish. Aquat. Sci. 40:43-51.
- Grimes, C. B. 1986. Reproductive biology of the Lutjanidae: A review. In J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management. Westview Press, Inc., Boulder. [See this volume.]
- Gulland, J. A. 1969. Manual of methods for fish stock assessment. Part 1. Fish populations analysis. FAO Fish. Tech. Pap. 38, Rev. 1, 67 p.
- _____. 1983. Fish stock assessment. A manual of basic methods. John Wiley & Sons, N.Y., 223 p.
- _____. 1984. Advice on target fishery rates. Fishbyte [ICLARM] 2(1):8-11.
- Hennemuth, R. C., J. E. Palmer, and B. E. Brown. 1980. A statistical description of recruitment in eighteen selected fish stocks. J. Northwest Atl. Fish. Sci. 1:101-111.
- Huntsman, G. R., and J. R. Waters. 1986. Development of management plans for reef fishes--Gulf of Mexico and U.S. South Atlantic. In J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management. Westview Press, Inc., Boulder. [See this volume.]
- Ikehara, I. I., H. T. Kami, and R. K. Sakamoto. 1970. Exploratory fishing survey of the inshore fisheries resources of Guam. In Proc. 2d CSK Symp., p. 425-437, Tokyo.
- Munro, J. L. 1983a. A cost-effective data acquisition system for assessment and management of tropical multitispecies multi-gear fisheries. Fishbyte [ICLARM] 1(1):7-11.
- _____. (editor). 1983b. Caribbean coral reef fishery resources. ICLARM Stud. Rev. 7, Manila, 276 p.
- Oda, D. K., and J. D. Parrish. 1981. Ecology of commercial snappers and groupers introduced to Hawaiian reefs. In E. D. Gomez, C. E. Birkeland, R. W.

- Buddemeier, R. E. Johannes, J. A. Marsh, Jr., and R. T. Tsuda (editors), Proc. 4th Int. Coral Reef Symp., Manila 1:61-67.
- Parrish, J. D. 1986. The trophic biology of snappers and groupers. In J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management. Westview Press, Inc., Boulder. [See this volume.]
- Pauly, D. 1983. Some simple methods for the assessment of tropical fish stocks. FAO Fish. Tech. Pap. N(234), 52 p.
- Polovina, J. J. 1986. A variable catchability version of the Leslie model with application to an intensive fishery experiment on a multispecies stock. Fish. Bull., U.S. 84(2).
- Polovina, J. J., and S. Ralston. In press. An approach to yield assessment for unexploited resources with application to the deep slope fishes of the Marianas. Fish. Bull., U.S.
- Polovina, J. J., and R. C. Roush. 1982. Chartlets of selected fishing banks and pinnacles in the Mariana Archipelago. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv. NOAA, Honolulu, HI 96812, Admin. Rep. H-82-19, 15 p.
- Pooley, S. G. 1986. Demand considerations in fisheries management--Hawaii's market for bottom fish. In J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management. Westview Press, Inc., Boulder. [See this volume.]
- Ralston, S. 1984. Biological constraints on production and related management issues in the Hawaiian deepsea handline fishery. In R. W. Grigg and K. Y. Tanoue, (editors), Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands, Vol. 1, May 25-27, 1983, University of Hawaii, Honolulu, p. 248-264. UNIHI-SEAGRANT-MR-84-01.
- _____. 1986. Mortality rates of snappers and groupers. In J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management. Westview Press, Inc., Boulder. [See this volume.]
- Ralston, S., R. M. Gooding, and G. M. Ludwig. In press. An ecological survey and comparison of bottom fish resource assessments (submersible versus handline fishing) at Johnston Atoll. Fish. Bull., U.S.

- Ralston, S., and K. Kawamoto. 1985. A preliminary analysis of the 1984 size structure of Hawaii's commercial opakapaka landings and a consideration of age at entry and yield per recruit. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812, Admin. Rep. H-85-1, 9 p.
- Ralston, S., and J. J. Polovina. 1982. A multispecies analysis of the commercial deep-sea handline fishery in Hawaii. Fish. Bull., U.S. 80:435-448.
- Ralston, S., and H. A. Williams. Unpub. Age, growth, and mortality of lutjanid and other deep slope fishes from the Mariana Archipelago. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.
- Sainsbury, K. J. 1986. Assessment and management of the demersal fishery on the continental shelf of north-western Australia. In J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management. Westview Press, Inc., Boulder. [See this volume.]
- Wetherall, J. A., J. J. Polovina, and S. Ralston. In press. Estimating growth and mortality in steady state fish stocks from length-frequency data. In D. Pauly and G. R. Morgan (editors), Length-based methods in fishery research. The ICLARM/KISR Conference on the Theory and Application of Length-Based Methods for Stock Assessment, Sicily, Italy, 11-16 February 1985. Vol. 1.

Demand Considerations in Fisheries Management-- Hawaii's Market for Bottom Fish

Samuel G. Pooley
Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
Honolulu, Hawaii 96822-2396

ABSTRACT

Fisheries management decisions are usually predicated on affecting the supply of fish at the point of harvest. However, changes in supply may have significant impacts on processors, wholesalers, and the final consumer.

Examination of Hawaii's market for bottom fish shows some price volatility in the short run, and quality premiums in both the short and long run. Long-term demand has been significantly positive, most closely associated with increasing population, tourist arrivals, and exports. Fisheries management decisions must take into account the impact of changing supply conditions on the availability and price of fresh bottom fish in the market.

INTRODUCTION

Fisheries management frequently affects not only the total volume of fish that reaches a market but also the timing and composition of supply. All three factors can affect the ex-vessel price of fish and thus commercial fishing incomes and, through the marketing chain, whole-sale and processor incomes and consumer budgets. Once the nature of demand is determined, any management scheme (e.g., supply constraint) can be evaluated with respect to its effect on prices and income. This paper describes the market for fresh snappers and groupers in the U.S. as a whole (primarily the east coast) but emphasizes Hawaii in

particular. Then the demand for fresh bottom fish in Hawaii is estimated through price flexibility functions. Finally, some management implications that derive from market demand estimation are explored.

DESCRIPTION OF THE MARKETS

International Markets

Fresh snappers are a high-value seafood product throughout their range: the east and gulf coasts of the mainland United States, Hawaii, the Caribbean, Australia, and New Zealand. Groupers are also an important seafood product in a number of these places, while jacks appear to be marginal commercial species but are valued for their sports fishing appeal. These species constitute the bottom fish management complex in Hawaii.

Annual landings of snappers on the mainland U. S. (primarily Florida) have declined recently to 4,200 metric tons (MT) valued at \$15 million in 1984. Landings of grouper and sea bass have been growing, with 1984 landings of 7,800 MT with an ex-vessel value of \$21 million ([U.S.] National Marine Fisheries Service (NMFS) 1985).

Hawaii's snapper-grouper market has always been considered marginal from a national perspective, but recent harvest records may change that assessment. There is, however, almost no competition between east coast and Hawaii snappers in either market area at this time, nor has there been substantial competition from imports. Imports of snappers and groupers to the U. S. have been relatively erratic in volume and appear to have a minimal impact on price determination for domestic species (Keithly and Prochaska 1984). Imports of snappers (and associated species) to the southeastern U. S. in 1984 were 3,800 MT, a record (Vondruska and Cunningham 1985).

In the U.S., snappers and groupers have a relatively low volume compared with apparently similar fish (e.g., west coast rockfish) and command considerably higher prices. The handline-harvested product is treated with considerably more respect than trawl-caught fish (although trawling for snappers has been instituted on the mainland U.S.) and receives appropriately higher prices. For example, April 1985 wholesale prices for red snapper at the Fulton Street Market in New York were in the range of \$3-\$5 a pound (roughly equivalent to Norwegian salmon), while sole and flounder were at \$1.50. In Hawaii the ex-

vessel price for all bottom fish averaged \$2.47 a pound (about \$3.50 wholesale) in 1984, a year of record supply, and prices for individual species reached over \$10 a pound during peak buying season for some species.

Economic studies of snappers and groupers emphasize the localized nature of their harvest and their primary markets. Cato and Prochaska (1976) reported a highly inelastic demand for fresh red snapper from Florida, indicating that there are relatively few substitutes for this species. Keithly and Prochaska (1984) found continued dominance of red snapper in the fresh market through 1982, with average prices for red snapper about double those for groupers. The primary source for growth in the price for snappers was growing total personal disposable income. More recent information shows that red snapper prices have been relatively constant over the past 4 years, while prices for other snappers and groupers have risen. This suggests that the market is broadening and that premiums for red snapper may diminish (Vondruska and Cunningham 1985). Rockfish from the west coast is already being marketed as snapper (at a substantially lower price) in some areas. Since harvests of red snapper may have already reached their biological limits in the United States, substitution of less heavily harvested species may be desirable, although this will have an unwanted income effect on commercial harvesters concentrating on red snappers.

It appears that the market for snappers in general is relatively independent of the demand for other seafood. It makes up a small percentage of average family household consumption (Keithly and Prochaska 1984), but the restaurant market for snappers may be relatively more important. Fluctuations in the price of snappers appear to be determined primarily by an exogenous domestic supply.

Snappers are also an important commercial sports fish on the east and gulf coasts (Huntsman et al. 1983), but this is not so in Hawaii (Samples et al. 1984). Huntsman points out that sports fishers prize large snappers, but that the commercial market has developed a niche for smaller fish, which may reduce the availability of larger, older snappers. One might conjecture that the development of the trawl fishery on the east coast, with its lower size selectivity, led to this development. In Hawaii, small snappers are also caught extensively by small-scale fishing vessel operators (part-time commercial and ostensibly recreational) for direct sale to households. Management problems appear to exist in both areas in terms of

allocation between groups of fishers, i.e., between full-time and part-time commercial fishers and with recreational fishers.

Hawaii Market

Hawaii's overall seafood market is well-known for relatively high prices based on local preference for a limited number of species of fresh fish. Included in this consumption bundle are a number of snappers, groupers, and jacks of which opakapaka, Pristipomoides filamentosus, is the most important. A fisheries management problem has developed because bottom fish and reef fish stocks in the main Hawaiian Islands (MHI) appear to be at or near maximum sustainable yields while market demand for bottom fish (especially in "up-scale" restaurants) has grown substantially in the past 5 to 10 years. The household market for small bottom and reef fish also continues to grow.

Hawaii's overall seafood market has been surveyed a number of times and is depicted in Figure 14.1. This diagram shows the market channels for all types of seafood in Hawaii. The bottom fish market, including fresh bottom and reef fishes and imported frozen snapper, follows these channels. Hawaii's retail market for fresh and frozen bottom fish and reef fish has been estimated at 2,750 MT (\$13.7 million), which constitutes approximately 11% of the final retail market. Frozen snapper imports to Hawaii (mainland U. S. and foreign) are estimated at 800 MT (1.8 million lb), \$2.5 million wholesale value (Higuchi and Pooley 1985; Pooley Unpub.; data from an unpublished 1981-1982 NMFS survey).

Figure 14.2 depicts retail outlets for all varieties of seafood in Hawaii and is representative for bottom fish. The Hawaii wholesale seafood business has three major components: (1) 10 major wholesale dealers who predominate in the fresh fish market; (2) 50 smaller fresh fish dealers who sell wholesale and retail; and (3) 50 wholesalers and brokers who handle frozen seafood imported from the U.S. mainland and foreign sources. The fresh bottom fish market operates around an auction in Honolulu, although sizable market channels exist outside the auction. The latter channels are based on bilateral exchange with negotiated pricing, typical of other fresh fish markets in the U.S. (Wilson 1980). The overall market might be termed one of contestable competition

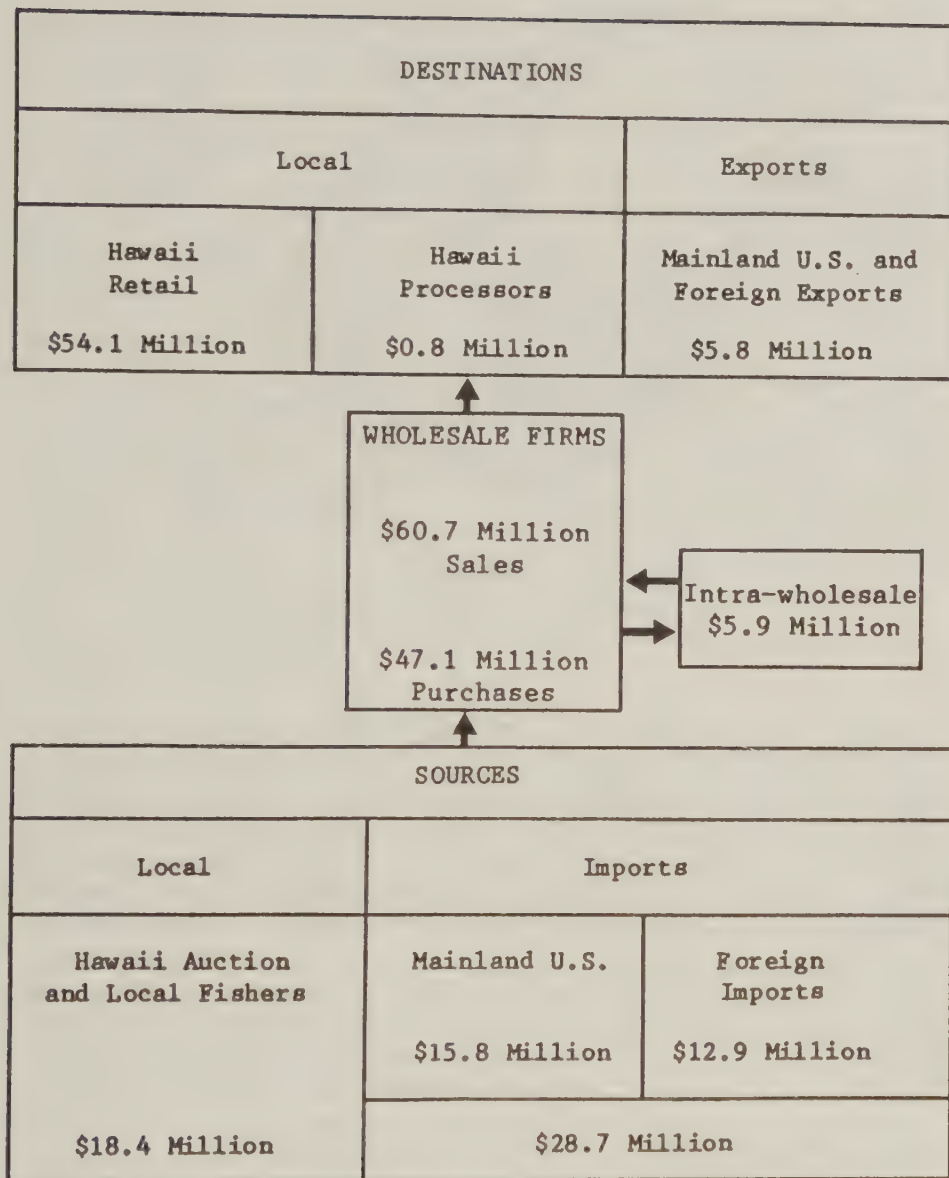


Figure 14.1 Market channels for Hawaii seafood sales, 1979 (millions of dollars)

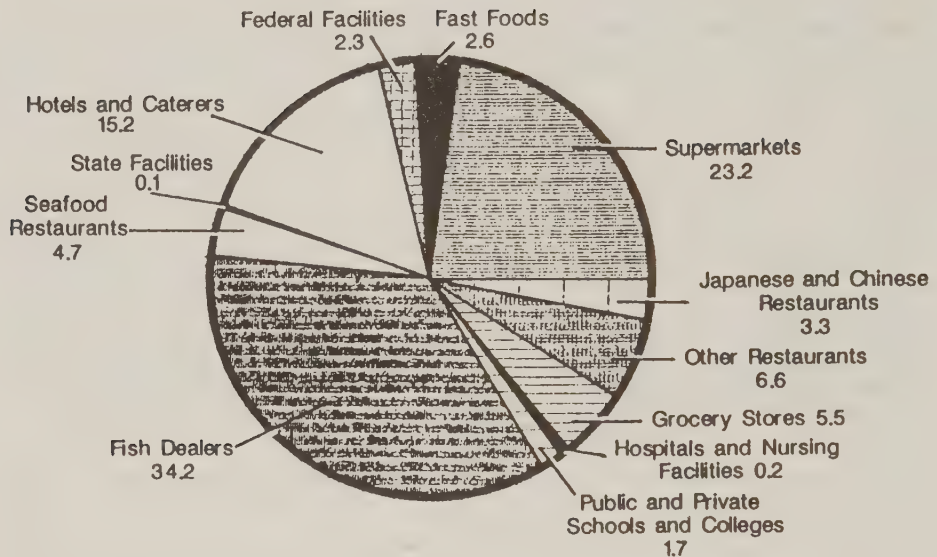


Figure 14.2 Retail outlets for all types of seafood in Hawaii (percentage of total revenue)

(Baumol 1982) in which a relatively small number of wholesale dealers of fresh and frozen seafood are able to generate economies of scale and scope in their product exchange functions. This reduces transactions and information costs while maintaining product heterogeneity, including an abundance of high quality, fresh seafood (Cooper and Pooley 1983). Retail prices are competitive.

Retail sales to Hawaii consumers include two components: regular purchases within a household's weekly food budget and a strong seasonal demand based on a cultural interest in large, red snappers for ceremonial occasions such as New Year's. This cultural demand also includes nonseasonal events such as weddings and birthdays. Favored fish in this category include the opakapaka, onaga, Etelis coruscans, and uku, Aprion virescens. The regular household component can be served by small bottom and reef fishes, by fillets of larger bottom fish, and by frozen snappers imported from the mainland United States and New Zealand. Although consumer substitution between product forms occurs, the frozen product is considered an inferior alternative for local bottom fish consumers. The price differential is substantial. In 1981 frozen snappers from New Zealand were entering Hawaii as fillets at \$1.40 per pound. During that year the average price for **whole**

bottom fish was \$2.30 per pound and for opakapaka alone, it was \$2.80 (NMFS unpublished wholesale market survey 1981-1982).

Restaurant demand for fresh bottom fish is centered on fresh opakapaka and is based on catering to "up-scale" tourist preferences (Takenaka et al. 1984; Monaghan 1985). Successful market promotion and a fairly regular supply of this species in large sizes has led to its introduction on restaurant menus as a high quality item. Substitution of other bottom fish and reef species has begun to occur, but this is not a preferred practice.

Exports of opakapaka and a few other large bottom fish have followed the growth of the tourist restaurant market, much as a market for red snapper moved north from Florida to New York years ago, but exports are still a fairly small component of the demand for local bottom fish. Fresh bottom fish is imported increasingly from American Samoa, Guam, Fiji, and Micronesia.

HAWAII PRODUCTION

From the production side, the bottom fish market is served by two types of Hawaii-based commercial fishing vessels as well as by import brokerage. Relatively large-scale (12-20 m, i.e., 45-65 ft), full-time commercial fishing boats ply the waters of the relatively distant (500-1,000 nmi) Northwestern Hawaiian Islands (NWHI). These modern vessels have the capacity to flood the fresh market at the conclusion of their 2- to 3-week trips, landing up to 7,000 kg of mixed bottom fish, but their boats have not developed an effective market for frozen product. This limits not only their catch total but their fishing range (Hau 1984). Opakapaka is the major catch of the NWHI fishery.

On the other hand, the MHI are the site of a mixed commercial and part-time fishery of relatively small vessels. Their catches fill a niche with smaller bottom and reef fishes. Their boats land <1,000 kg and usually much less. The MHI vessels are frequently operated on extra-economic rationales and are faced with substantial resource pressure. Both the NWHI and the MHI vessels compete in the same fresh fish market, although size composition tends to allocate the larger fish of the NWHI catch to restaurants and the smaller fish of the MHI catch to the household market (Table 14.1). This competition between large- and small-scale vessels, each representing

TABLE 14.1

Hawaii bottom fish sales, 1984 (numbers in pounds rounded). Scientific names are given in the text. MHI = Main Hawaiian Islands; NWHI = Northwestern Hawaiian Islands. (Source: Western Pacific Regional Fishery Management Council 1985:152)

Group/ Species	Landings		Prices		Total Revenue
	MHI	NWHI	MHI	NWHI	
Group 1					
Uku	146,100	10,600	\$2.30	\$2.50	\$362,500
Ulua	59,700	80,300	1.90	1.05	197,700
Subtotal	205,800	90,900	2.18	1.22	560,200
Group 2					
Opakapaka	211,600	331,900	3.35	2.70	1,605,000
Gindai	4,600	2,800	2.20	2.95	18,400
Hapuupuu	55,300	98,100	1.80	1.65	261,400
Lehi	16,300	0	2.30	0.00	37,500
Subtotal	87,800	432,800	2.97	2.46	1,922,300
Group 3					
Onaga	190,700	6,500	4.00	2.95	782,000
Ehu	36,800	5,000	2.75	2.10	111,700
Kalekale	23,800	2,500	2.20	1.60	56,400
Subtotal	251,300	14,000	3.65	2.40	950,100
Other	165,000	8,600	1.25	1.10	215,700
Total	909,900	546,300	2.65	2.25	\$3,595,900

small business enterprises, has increased pressure for government regulation, including limited entry (Western Pacific Regional Fishery Management Council (Council) 1985; Pooley Unpub.).

Such institutional factors should be considered in fisheries management planning but generally are not. Since the supply of fish is the major variable affected by fishery management plans, its effect on the market needs to be investigated. In the next section, the demand for fresh bottom fish in Hawaii is estimated with a view toward understanding the relationship between fisheries

production and marketing. The final section examines the economic impact of regulated changes in supply.

ECONOMIC DEMAND

The demand for fresh bottom fish represents a specific behavioral relationship: Consumers are said to determine the quantity demanded of a particular type of fish based on a number of demand determinants (characteristics). The primary determinant is the price of the fish, but other determinants include the price of substitutes, the size and quality of the fish, and seasonal considerations. Long-term characteristics include per capita disposable income and the size of the market, i.e., the population. The data available for estimating the demand for Hawaii's bottom fish are based on wholesale purchases of fresh product in the round. Therefore, in this paper a short-run price formation function of the following general form is utilized.

$$P_f = f(Q_f, Q_a, SD, CD)$$

where P_f is the ex-vessel price per pound of a particular type of bottom fish, Q_f is the market quantity of that type of fish, Q_a is the market quantity of substitute (alternative) species, SD is a dummy variable representing product quality based on the source of the product, and CD is a dummy variable representing seasonal consumer demand. In the short run, population and income are assumed to be fixed. Wholesale buyers make their offer prices to harvesters based on expectations of conditions in the final consumer markets. This offer is not significantly affected by inventories in a fresh fish market. Therefore, the price formation curve is mathematically equivalent to the inverse of the demand curve.

The price-quantity relationship can be depicted as a linear or logarithmic relationship and through two summary measures: (1) elasticity, which is not directly applicable to wholesale market analysis, and (2) its inverse, a price flexibility coefficient, F_p , which measures the percentage rate of change of a product's price relative to the rate of change of the product's quantity sold, i.e.,

$$F_p = - \frac{\%dP_f}{\%dQ_f} * 100$$

A logarithmic transformation of the price and quantity variables translates regression coefficients directly into estimates of elasticity or price flexibility, depending on the form of the equation.

The problem of explanation for seafood market price-quantity relationships is not trivial and is not unlike problems in understanding population dynamics and other features of fish stocks where observable phenomena have an uncertain relationship to underlying forces. The seafood market is a complex institution embedded in a network of social structures. The quantitative measures of market behavior are limited and interpretation of market forces is frequently contested. Previous explanations of seafood markets in Hawaii have explored the social side of fresh fish auctioning (Peterson 1973), the nature of market channels (Garrod and Chong 1978), the econometrics of a fresh fish cooperative (Hudgins 1980), industrial structure (Adams 1981), and characteristics of market transactions (Cooper and Pooley 1983). This paper builds on those explanations but does not completely "explain" the demand for fresh bottom fish. Although microeconomic theory of price determination has been developed in great detail (it is probably the most elaborate theoretical structure within economics), it is a relational theory of static aggregations of interpersonal interactions in an implicitly formulated general equilibrium framework. Therefore, the best that econometric analysis of market price can hope to accomplish is to reveal the pattern of exchange characteristics that can be directly observed, i.e., the variations in price and quantity.

None of the characteristics that describe the seafood market has causal properties in and of itself; each is a manifestation of underlying human activity. On one side, commercial fishers require monetary equivalents for their harvest; on another side there is the institutional arrangement of wholesale dealers in transacting commodity exchange; and on a third side are the preferences of consumers concerning their consumption expenditures. Econometric analysis of the wholesale market for fresh bottom fish distills this behavior and social structure into a limited number of quantitative variables, but it is examination of, and experience with, the particular characteristics of this market, and the existence of a lengthy intellectual tradition pertaining to microeconomic analysis, that make this distillation practical and informative.

Assuming a competitive equilibrium market, price and quantity data represent the intersection of supply and demand where only the point of equality is revealed. Therefore, a time series is subject to an identification problem: What is being discovered, the demand or the supply relationship? This problem is solved in short-term analysis of a highly perishable product like fresh seafood by the prior restriction that supply be independent of price. Demand is considered stable over a year. The exogenous determination of quantity supplied to the market allows statistical determination of the demand curve from market data.

MARKET DATA

Basic data for this analysis come from two sources. The only publicly available long-term source of price and quantity information is the State of Hawaii's landing records. The Hawaii Division of Aquatic Resources (HDAR) requires all commercial fishers in Hawaii to report their sales of fish on a monthly basis. These data are summarized and provide a monthly time series of market volume and price by individual species. The HDAR data were

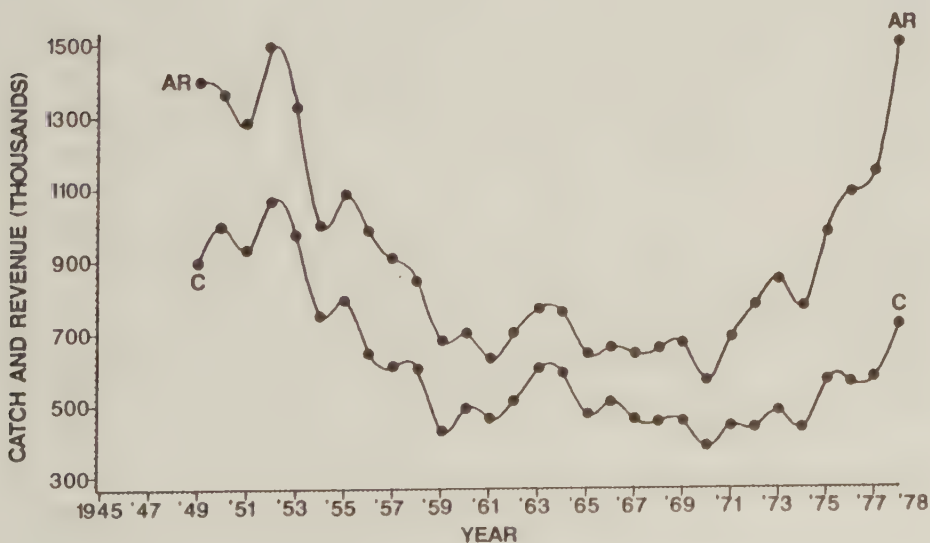


Figure 14.3 Bottom fish landings in Hawaii, 1949-1978 (AR = adjusted revenue in 1981 prices; L = catch in 1,000s of pounds)

TABLE 14.2

Hawaii fresh fish market: Monthly summary
statistics, 1965-1982. N = 216

Variable Description	Variable Name	Average	Standard Deviation	Coeffi- cient of Variation (%)	Loga- rithmic Mean
Pounds Sold					
Bottom fish	QBTTM	37,000	15,000	41	3.53
Group 1	QBTTM-G1	14,000	7,000	49	2.52
Group 2	QBTTM-G2	16,000	9,000	60	2.57
Group 3	QBTTM-G3	7,000	4,000	51	1.86
Tunas	QTUNA	825,000	621,000	75	6.46
Mahimahi and wahoo	QMAHI/ONO	21,000	15,000	71	2.75
Average Monthly Prices					
Inflation-Adjusted Prices Per Pound (December 1982 Price Level)					
Bottom fish	PBTTM[R]	\$2.09	0.42	20	0.72
Group 1	PBTTM- G1 [R]	1.65	0.35	21	0.48
Group 2	PBTTM- G2 [R]	2.01	0.59	29	0.66
Group 3	PBTTM- G3 [R]	3.14	0.54	17	1.13
All fresh fish	PFISH[R]	1.11	0.44	40	0.02
Fresh fish, excluding skipjack tuna	PFISH- SJ [R]	1.55	0.35	23	1.55
Hawaii Demographics					
Defacto population	POP	900,000	95,000	11	6.79
Resident population	RES	841,000	31,000	53	6.73

(Continued)

TABLE 14.2 (Cont.)

Variable Description	Variable Name	Average	Standard Deviation	Coefficient of Variation (%)	Logarithmic Mean
Average daily visitor census	VISIT	59,000	--	--	3.91
Real disposable personal income per capita (monthly)	RDINC	\$876	\$112	13	6.77
Consumer dummy:					
1=Jan., Dec., Mar., or Apr.;					
0=normal demand					
	CD	0.25	--	--	--

available for bottom fish through December 1982. This analysis uses the data beginning in 1965, the year in which Hawaii's overall commercial fishery "bottomed out" following much higher sales following World War II. Figure 14.3 presents bottom fish landings in the postwar period and Table 14.2 presents average monthly values. The HDAR revenue figures are "adjusted" for inflation by basing all prices on the December 1982 consumer price index for Honolulu.

For the long-term analysis, monthly Hawaii population and tourist arrival information was obtained from regular State of Hawaii Department of Planning and Economic Development reports. Hawaii has experienced considerable growth in population and visitor arrivals (averaging roughly 2.5% annually since 1965), and the variables are highly correlated ($r = 0.92$). Data on real disposable personal income per capita (RDINC) were obtained from U.S. Bureau of the Census and Hawaii Department of Planning and Economic Development sources. The RDINC has declined since 1976 due to structural and cyclical economic factors in Hawaii's economy.

The source of short-term market information is the Council, which has a regular monitoring program of wholesale bottom fish purchases from Hawaii's commercial

fishery. These data represent a large proportion of the entire fresh fish market in Hawaii and were collected throughout 1984. However, to protect the confidentiality of their source, the quantity data have been scaled to levels approximate to an estimate of the overall market volume. The data were aggregated into weekly quantities and prices, and summaries appear in Table 14.3.

TABLE 14.3

Hawaii fresh bottom fish market: Weekly, 1984.
(MHI = main Hawaiian Islands; NWHI = Northwestern
Hawaiian Islands)

Variable Description	Variable Name	Average	Standard Deviation	Coeffi- cient of Variation (%)	Loga- rithmic Mean
Pounds Sold					
Bottom fish	QBTTM	24,700	11,200	45	9.9
Group 1	QBTTM-G1	5,700	3,900	68	8.42
Group 2	QBTTM-G2	13,900	7,500	54	9.34
Group 3	QBTTM-G3	5,100	3,500	69	8.25
MHI	QMHI	14,300	8,000	56	9.38
NWHI	QNWHI	10,300	7,000	68	8.98
Average Weekly Prices					
			Price Per Pound		
Bottom fish	PBTTM	\$2.91	0.74	25	1.04
Group 1	PBTTM-G1	2.12	0.75	35	0.69
Group 2	PBTTM-G2	2.95	0.80	27	1.05
Group 3	PBTTM-G3	4.03	0.89	22	1.37
MHI	PMHI	3.31	0.88	27	1.16
NWHI	PNWHI	2.45	0.74	30	0.86
Consumer dummy: 1=peak season; 0=normal demand	CD	0.17	--	--	--

For both the long-term and short-term analysis, a consumer dummy variable takes on a value of 1 during peak demand periods (Christmas, New Year's, and Easter) and 0 otherwise.

METHODOLOGY

The basic question is: How do seafood consumers (or wholesale dealers acting on expectations of consumer behavior) react to changes in the supply of fresh bottom fish? If consumers have a number of substitutes for fresh bottom fish, then we can expect the price formation function to be relatively flat as consumers adjust their purchases to price. On the other hand, if consumers accept few substitutes, we would expect a steep demand curve and high price flexibility. It appears that the former is the case, but the purchase decision appears to be a "limited choice" decision, i.e., there is little likelihood of substitution to apparently comparable fresh fish when prices rise, and the range of purchases is limited.

With the assumption that the quantity supplied to the market by the commercial fishery is independent of price, at least in the short run, a simple linear model using ordinary least squares regression techniques can be applied to the price and quantity data to estimate the price formation curve. Although this is a rudimentary technique, it appears to be viable in this case.

Previous analysis of similar data indicated a problem with serial correlation of the residuals from regression analysis of the time series (Higuchi and Pooley Unpub.). Therefore, the data are transformed through an autoregressive lag technique called the Hildreth-Lu procedure, which corrects for such serial correlation. The autoregressive factor, g , is indicated for each equation. The equations are in the appendix.

Price flexibility coefficients are calculated from the regression coefficients of the price equations. Logarithmic conversion of the data provides continuous estimates of price flexibility from the regression coefficients. The logarithmic form also deals with some nonlinearities in the demand function. Although it is unlikely that consistency of the price flexibility parameter across the entire range of quantity applies, the results of the logarithmic and the linear models (equations not shown) showed no significant differences.

Substitution is examined for three groups of Hawaii's bottom fish taken from depth-groupings (Ralston 1979). All but two of the species are snappers.

- Group 1: uku, Aprion virescens
ulua, Caranx spp. (jacks)
- Group 2: gindai, Pristipomoides zonatus
hapuupuu, Epinephelus quernus (sea bass)
lehi, Aphareus rutilans
opakapaka, P. filamentosus
- Group 3: ehu, Etelis marshi
kalekale, P. sieboldii
onaga, E. carbunculus

These groups, based on depth habitats, reflect neither commercial harvest nor market comparability characteristics. A simple factor analysis of prices and quantities for the nine species could find no stronger relationships, and an alternative specification of groups showed no stronger overall average bottom fish price-quantity relationship than the groups chosen, although individual group prices were better explained in some cases.

RESULTS

Short Run Demand, 1984

The weekly data for 1984 show a statistically significant negative price-quantity relationship for fresh bottom fish sales in Hawaii. The average weekly price of all bottom fish is negatively correlated with the weekly quantity supplied, and the relationship is statistically significant at the 99% confidence level (Equation 1). The same is true for monthly aggregations (Equation 2). The consumer dummy variable is also significant in both situations. Variation in quantity supplied and in the consumer dummy variable statistically explains half the price variation ($R^2 = 53\%$ for the weekly data and $R^2 = 59\%$ for the monthly data). The weekly price-quantity relationship, corrected for seasonal effects, is plotted in Figure 14.4. Interestingly, the price-quantity relationship for weekly bottom fish sales in 1984 is almost exactly the

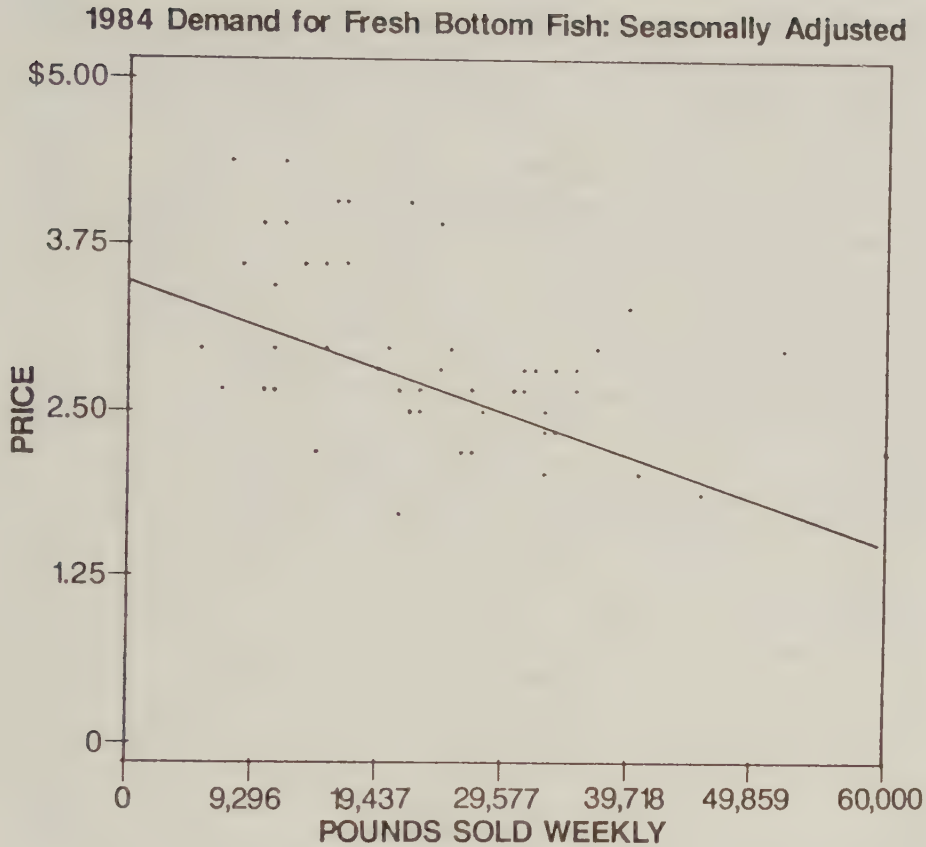


Figure 14.4 Demand for fresh bottom fish, 1984

same as a previous analysis based on 1976-1977 weekly sales (Higuchi and Pooley Unpub.).

The price flexibility coefficient calculated from the regression equation on weekly data is 23%, while the monthly coefficient is 42% (calculated from Equations 1 and 2). This means that price does not vary as much as quantity. The average weekly market sales are 11 MT (25,000 lb) with a standard deviation of 5 MT (11,000 lb). A change in landings of one standard deviation raises or lowers price a predicted 30 cents, approximately 10%. Price volatility is occasionally much greater than predicted by this simple statistical technique. In most cases, wholesalers ride out reductions in the quantity supplied in the short run through short-term "inventories." However, if quantity is suppressed or increased for several weeks, then such discounting cannot be main-

tained and price will fluctuate more widely. This is shown by the higher price flexibility coefficient for monthly aggregations. The range in actual prices (one standard deviation) was $\pm \$1.13$, or a price flexibility of 100%.

Central to the fresh bottom fish market in Hawaii are quality premiums: Fish handled carefully and those caught closer to the Honolulu market have longer shelf life and commensurately higher prices. Although this price formation behavior can be observed at the Honolulu auction, specification of a quality factor is extremely difficult because it is only reflected in the judgment of bidders and final users. Fish caught in the MHI are caught nearer to the market (thus have longer shelf life) and are caught in smaller numbers (thus maximizing the potential for individual handling). This advantage is offset by the fact that NWHI fish are generally larger and thus have a larger yield and because the NWHI vessels have better refrigeration. Smaller fish are valued by many local consumers because they can be used as single meals, but larger fish are prized by restaurants for their fillets.

Using the 1984 market sample and discriminating between fish landed from the MHI and the NWHI, the conflicting effects of quantity and quality are revealed. A pooled cross-section time-series approach was used to test for price differences based on location of catch. Average weekly sales for each species group were divided into MHI and NWHI and pooled together into a data set where a dummy variable was used to specify the MHI fish. The source dummy is statistically significant (Equation 3) and indicates that fish landed from the MHI can expect approximately a 50% price "bonus" because of quality consideration. However, some fish from the NWHI are handled well and receive comparable prices and paradoxically, the more fish landed from the NWHI (variable QN:Q), the higher the average price. (This is explained by short-run supply effects whereby NWHI vessel operators attempt to land during peak demand periods or when rough weather restricts the smaller MHI vessels from fishing.)

Breaking quantity sold into species groups substantially improves the price formation function (Equation 4). The strongest simple correlation comes from the shallow water group (ulua and uku), which receives the lowest average price. Price flexibility for each of the species groups is also estimated (Equations 5-7).

One expects the determination of price to be improved by examining the market by species group. However, this

leads to another interesting question: To what extent do landings of other species affect the price of a particular species? This relationship is termed cross-elasticity, and its effect is represented by the statistical significance of the regression coefficient for the quantity supplied of the alternative species group. These results (Equations 8-10) show a fair degree of separability for the high-priced groups (opakapaka and onaga), since the cross-elasticities are not large.

Examination of data for 1976-1977 shows almost no cross effects with other types of fresh seafood in Hawaii, e.g., tuna, mahimahi, and wahoo (Higuchi and Pooley Unpub.). Landings of one bottom fish group have some effect on the prices in the other bottom fish groups. However, landings in the rest of the fishery (i.e., tunas, mahimahi, wahoo, and marlins, etc.) seem to have no noticeable influence in the short-term price formation for bottom fish, which supports the idea that their short-term demand is relatively independent (see also Equation 14).

Another question important to Hawaii's commercial fishery is: To what extent is market price determined by relative landings from the two main harvesting areas? The strongest correlation with overall market price is with NWHI landings, which is not surprising since they provide larger fluctuations in volume (Equation 11). However, a price determination equation for the MHI alone shows that NWHI landings appear to have little causal effect on MHI prices, compared with the effect of MHI landings and the consumer dummy variable (Equation 12). Because landings from the MHI are considered of higher quality, their volume appears to determine their own price level independently of NWHI landings.

Long-Term Demand, 1965 to 1982

In the short run, one can assume that consumer demand for a product, such as fresh bottom fish, is rather stable, since consumer preferences are themselves relatively stable. However, in the long run, a number of factors will affect the market demand for a product. First, the size of the market may change through population growth or expansion into new markets such as restaurants, retail promotion, and exports. Second, the characteristics of consumers may change through a change in their disposable income (income after taxes), or their basic preference structures may change through advertis-

ing, perceived health effects, generational shifts, etc. Summary statistics for this period appear in Table 14.2.

Not surprisingly, the statistical information suggests that the strongest long-term impact on the price for bottom fish is the growth of Hawaii's *de facto* population (resident and tourist combined). The simple correlation between the resident population and the inflation-adjusted price for fresh bottom fish was statistically significant, $r = 0.441$. Relationships with actual landings, the seasonal dummy variable, and real disposable income per capita were much weaker. However, when placed in a linear regression format, seafood volume and the consumer seasonal dummy variable, as well as resident population, are highly significant, while real disposable income per capita is not (Equation 13). These variables "explain" 60% of the variation in the inflation-adjusted price of bottom fish over the period 1965-1982.

I also investigated the cross effect of other species groups on bottom fish prices and somewhat surprisingly found a strong negative relationship between local landings of tuna (ahi--yellowfin and bigeye tunas, and aku--skipjack tuna) and the price of bottom fish (Equation 14). A regression on the price of bottom fish with bottom fish, tuna, and mahimahi or wahoo landings (using the logarithmic transformations as before) as well as the consumer dummy variable "explains" 34% of the monthly variation in price over the 18-year period. The negative effect of tuna on bottom fish price suggests some substitution, while the positive effect of mahimahi and wahoo indicates the parallel marketing of these white-fleshed species (Takenaka et al. 1984). A 22,700 kg (50,000 lb) increase in the total supply of tuna reduces bottom fish prices by only 1.8 cents; however, this change in supply is <10% of the standard deviation for tuna landings.

Finally, although prices for fresh fish in Hawaii track together to a certain extent (Equation 15), the relationship is weaker than one might expect. Over the long term, the price of bottom fish rose more rapidly than the price of all fresh fish (Figure 14.5) except skipjack tuna, which increasingly shifted from the cannery to the fresh market in Hawaii. The nonskipjack tuna prices rose at an annual rate of 1.5%, of which bottom fish prices rose by 3.1% after adjustment for inflation. In terms of the three species groups, prices tracked quite closely for the two groups with the highest percentage of catch in the NWHI, i.e., the ulua-uku and opakapaka groups (Table 14.4). The opakapaka group had the strongest time-trend

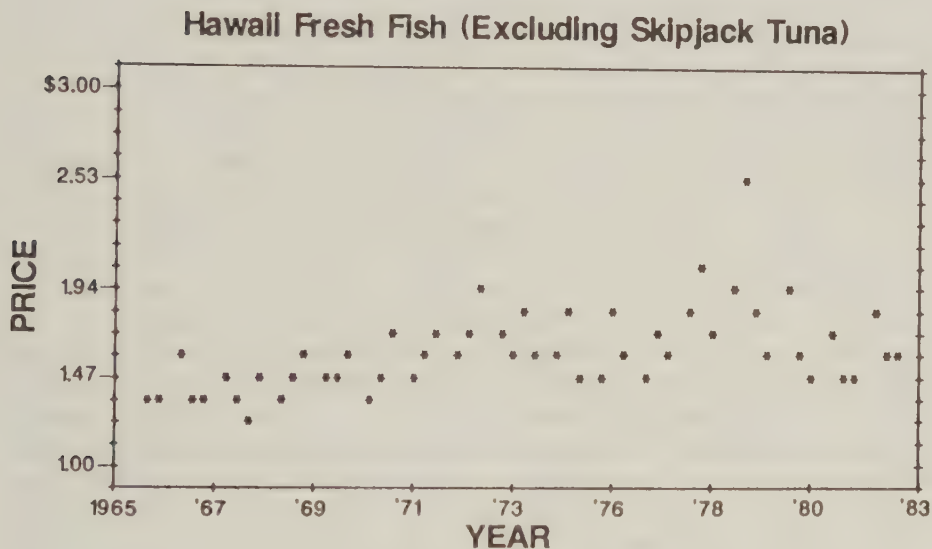
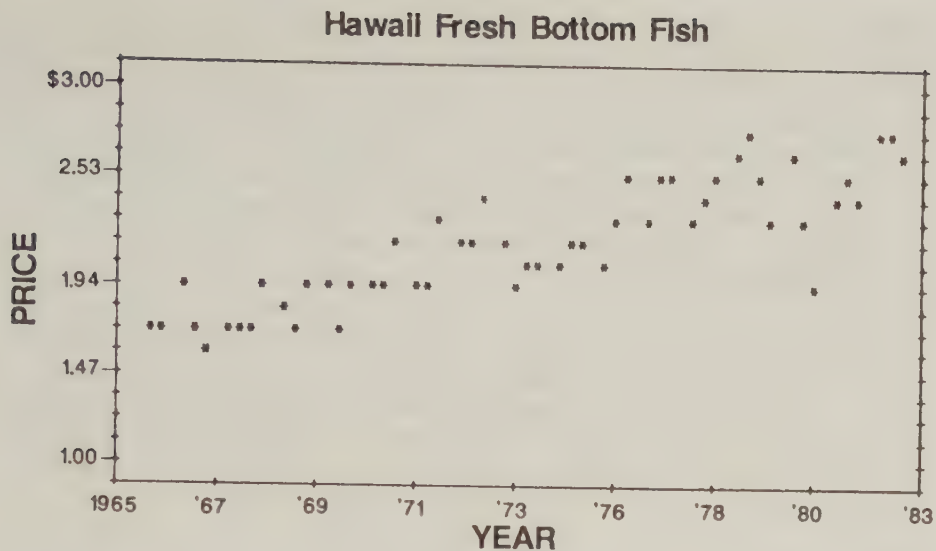


Figure 14.5 Inflation-adjusted prices for fresh bottom fish and all species, excluding skipjack tuna, Hawaii 1965-1982

($r = 0.809$) and the onaga-ehu group had the lowest ($r = 0.302$). This also suggests the importance of the restaurant market, which has promoted opakapaka, compared with the traditional home market, which prizes onaga, for growth in the demand for fresh bottom fish in Hawaii.

TABLE 14.4

Hawaii bottom fish prices (inflation-adjusted) 1965-1982 simple correlations. All correlations are significant at the 99.9% confidence level. Monthly average prices for bottom fish and bottom fish groups

	Simple Correlation Coefficients			
	PBTM	PBTM-G1	PBTM-G2	PBTM-G3
PBTM[R]	1			
PBTM-G1 [R]	0.888	1		
PBTM-G2 [R]	0.864	0.731	1	
PBTM-G3 [R]	0.643	0.454	0.523	1
Month (1-216)	0.664	0.596	0.809	0.302

CONCLUSION

The evidence obtained from examining the interaction of pounds sold and prices in Hawaii's fresh fish market suggests that factors affecting the supply of fresh bottom fish and exogenous changes in Hawaii's markets, especially in the growth of the domestic and export markets, may have important effects on prices. As a result, to the extent that wholesale prices are parallel to ex-vessel prices, the incomes available to the commercial fishery will be affected. The commercial fishers in Hawaii have long worried about large swings in the price for fresh fish, particularly on the "down" side, such that the total revenue to the vessel (and hence its captain, crew, and owner) is actually reduced despite increased landings. In particular, MHI vessel operators worry that landings from the larger vessels which ply the NWHI and make less frequent landings will flood the market and reduce income for the MHI fishery. The same problem also affects the NWHI vessel operators who depend on some type of price stability to rationalize their fishing schedules.

The average "swing" in the Hawaii bottom fish market in terms of pounds sold, prices, and gross revenues is

substantial: pounds and revenue vary by 45% weekly, while prices vary by 25% (Table 14.3, coefficient of variation). In other words, although prices and quantities tend to be negatively related, there are sufficiently large exogenous effects on the market so that the income effects of "swings" may be considerable. Thus not only are Hawaii's commercial fisheries related in terms of the resource, they are linked in the market.

A particularly visible example is the effect of the newly developed NWHI bottom fishery. Using somewhat hypothetical cost and catch rate data, one NWHI vessel unloads a total of 4,500 kg (10,000 lb) of mixed bottom fish at the end of a normal trip, based on 1984 data. The captain can expect an average price of \$2.45 per pound for the catch, \$25,000 in gross revenue, a crew share of some \$10,000, and a net income (after all expenses) of approximately \$1,500 (Hau 1984; and unpublished vessel simulators by Pooley). At the same time, some 20-40 MHI vessels (fishing relatively full-time) can expect a price of \$3.31 based on their total landings of 6,400 kg (14,000 lb). This would represent weekly crew incomes of \$400 per person and net vessel incomes of \$300 per vessel after expenses (data from NMFS cost-earnings surveys (Lyman and Hawaii Opinion 1984) and unpublished vessel simulators).

If an additional NWHI vessel off-loaded during a particular week, total landings would increase by 4,500 kg (10,000 lb), increasing total market volume by 42%. Average prices would fall approximately 10%: for the NWHI vessels to approximately \$2.20 and for MHI vessels to \$3.00 (using Equation 1 and Table 14.3). The effect on gross sales is still positive: Gross sales increase from \$70,800 to \$86,000, or 17.5%. However, the effect on the individual vessels is, of course, negative: Each NWHI vessel gets \$2,500 less than otherwise and each MHI vessel gets \$150 less. This translates into smaller crew shares and net returns per vessel. Similar effects could occur from other factors which would increase landings for one sector of the overall fishery and not another, such as increased sales by "recreational" fishers.

These competitive effects are well known and are a substantial reason why the fishing industry favors some form of management. Fishery managers, however, usually concentrate on the biological effects of overfishing on fish stocks without as much attention to the overall economic effect of such decisions. Yet simply by affecting the timing of total landings (optimized at whatever long-run level), fishery managers can have substantial

effects on short-run liquidity and long-run profitability for harvesters and processors.

Seasonal closures and quotas (including the currently popular share system known as "individual fishermen's quotas"), which tend to "clump" landings early in the quota period, may depress incomes for vessels landing any species subject to price flexibility. (There are of course other effects.) Consumers, on the other hand, would be faced with higher prices during the off-season, during which MHI vessels would receive relatively higher prices. While such price effects are frequently not relevant for "industrial" fisheries such as tuna, shrimp, and rockfish, it is certainly the case for fresh snappers.

For example, in Hawaii's fishery, a 2-month closure of the NWHI with no effect on total annual landings (implying increased effort during the "on-season" and no shifting of effort into the MHI) would increase weekly landings during the on-season by 910 kg (2,000 lb). This would have only a marginal impact on prices, which might be expected to decline by 5 cents. However, for the NWHI vessels, which are incurring larger costs during the on-season, this will affect total net income, reducing their annual gross sales by \$27,500. During the off-season, the amount of bottom fish available in the Hawaii market would decline by 4,800 kg (10,500 lb) per week. This would increase prices by 28 cents per pound, on average, and thus increase the value of the MHI catch during the off-season by a total of \$40,000. The net gross sales effect of the price changes in the two seasons would be almost exactly offset for the MHI fleet.

The Council calculates that the maximum sustainable yield (MSY) for the NWHI fishery is approximately 320,000 kg (700,000 lb) of mixed bottom fish (Council 1985). This is approximately 30% more than was landed in 1984 as the fishery was still developing. This increase in landings might be expected to depress market prices until additional export markets are found: The price effect would be 19 cents, so that gross revenue would increase by only 20%.

If the fishery stabilizes at MSY over the long term, and Hawaii's domestic market grows because of population effects, then there would be a positive price effect. The State projection of population in 1990 is for a 10% increase. The price effect of a growing market would be 45 cents (15.6%), raising gross revenue on the MSY level of landings by \$300,000.

The market for fresh bottom fish in Hawaii appears to be much as the markets for snappers are throughout the world--a market for a product highly valued with significant quality premiums. Short-run (weekly) fluctuations in landings are reflected in price but perhaps less than the commercial fishers might expect. Medium-run (monthly) fluctuations are greater and indicate the kind of problems that might arise with management measures affecting the scheduling of landings (such as annual catch quotas or seasonal closures). At the same time, the market seems capable of domestic expansion, which increases the potential biological pressure on fish stocks. Proposals for managing Hawaii's bottom fish may have to reflect the quality premiums that exist for fish coming from the MHI as well as the weak substitutability between species, especially in the case of opakapaka (Pooley 1985). Whether a high-quality frozen product would be acceptable in Hawaii and whether it would compete with the MHI catch or with frozen snapper imports is another important issue.

The total income effects shown in this section are not dramatic because of the relatively low short-term price flexibilities and small landings volume in Hawaii's fishery. However, for this small-scale industry, which is similar to other snapper fisheries throughout the world, the individual effects are important. Perhaps the state of fisheries science is not sufficiently precise to emphasize the effect of the market on the impact of fisheries regulations and development, but a general awareness of such effects would seem to be an important contribution to obtaining the highest level of social value from these unique resources.

NOTES

Appreciation but neither blame nor responsibility to three reviewers: L. Hudgins, D. Squires, and J. Waters.

1. The recorded supply of fresh bottom and reef fish in Hawaii is only some 1,250 MT (2.5-3 million lb). The discrepancy with the retail survey is not explained but may relate to double counting on the retail side (i.e., resale) and undercounting on the harvest side (through "back door" sales).

2. Disequilibrium models are not applicable to fresh fish markets.

3. Data manipulation was assisted by Jim Baxter, computer aid, and Wesley K. Higuchi, mathematics aid.

4. Kurt Kawamoto of the Western Pacific Regional Fishery Management Council was responsible for this data collection.

5. A value of -1.0 on the regression coefficient for quantity purchased (Qd) indicates price and quantity changes are strictly (negatively) proportional and the price flexibility coefficient is 100%. A value less than -1 indicates an inelastic demand where price changes relatively more than pounds sold. A coefficient of -2.0 translates into a price flexibility of 200%. A value between 0 and -1 indicates an elastic demand where pounds sold change relatively more than price. A coefficient of 0 shows a price flexibility of 0 and a coefficient of -0.50 translates into a price flexibility of 50%. However, translation of elasticities into price flexibilities, especially between ex-vessel and retail levels, is somewhat suspect (Manderscheid 1964; Houck 1965).

BIBLIOGRAPHY

- Adams, M. F. 1981. Competition and market structure in the Hawaii fish industry. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, Admin. Rep. H-81-5, 20 p.
- Baumol, W. R. 1982. Contestable markets: An uprising in the theory of industry structure. *Am. Econ. Rev.* 72-1:1-15.
- Cato, J. C., and F. J. Prochaska. 1976. The Gulf of Mexico commercial and recreational red snapper-grouper fishery: An economic analysis of production, marketing, and prices. In H. R. Bullis, Jr. and A. C. Jones (editors), *Proceedings: Colloquium on snapper-grouper fishery resources of the western central Atlantic Ocean*, p. 95-128. Texas A&M Univ. Sea Grant Coll. and Mississippi-Alabama Sea Grant Consortium. Fla. Sea Grant Coll. Rep. 17.
- Cooper, J. C., and S. G. Pooley. 1983. Characteristics of Hawaii's wholesale seafood market. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, Admin. Rep. H-83-22, 33 p.
- Garrod, P. V., and K. C. Chong. 1978. The fresh fish market in Hawaii. Dep. Pap. 23, Hawaii Agric. Exp. Stn., Coll. Trop. Agric., Univ. Hawaii, 24 p.
- Hau, S. 1984. Economic analysis of deep bottom fishing in the Northwestern Hawaiian Islands. In R. W. Grigg and K. Y. Tanoue (editors), *Proceedings of the Second*

- Symposium on Resource Investigations in the Northwestern Hawaiian Islands, Vol. 1, May 25-27, 1983. Univ. Hawaii, Honolulu, Hawaii, p. 265-282. UNIHI-SEAGRANT-MR-84-01.
- Higuchi, W. K., and S.G. Pooley. 1985. Hawaii's retail seafood volume. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, Admin. Rep. H-85-6, 16 p.
- _____. Unpub. Market responsiveness in Hawaii's commercial fishery. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.
- Houck, J. P. 1965. The relationship of direct price flexibilities to direct price elasticities. J. Farm Econ. 47(3):789-792.
- Hudgins, L. L. 1980. Economic model of a fisheries market with endogenous supply: The Hawaii skipjack tuna case. Ph.D. Dissertation, Univ. Hawaii, Honolulu, 114 p.
- Huntsman, G. R., C. S. Manooch III, and C. B. Grimes. 1983. Yield per recruit models of some reef fishes of the U.S. South Atlantic Bight. Fish. Bull., U.S. 81:679-695.
- Keithly, W. R., and F. J. Prochaska. 1984. The demand for major reef fish species in the Gulf and South Atlantic regions of the United States. Louisiana State Univ. Working Pap., 14 p.
- Lyman, A. L. Inc., and Hawaii Opinion, Inc. 1984. Economic and financial analysis of Hawaii's longline and handline fisheries. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, Admin. Rep. H-84-17C, var. pag.
- Manderscheid, L. V. 1964. Some observations on interpreting measured demand elasticities. J. Farm Econ. 46(1):128-136.
- Monaghan, C. 1985. Seafood heaven. United 30:10:86-184.
- Peterson, S. B. 1973. Decisions in a market: A study of the Honolulu fish auction. Ph.D. Dissertation, Univ. Hawaii, Honolulu, 287 p.
- Pindyck, R. S., and D. L. Rubinfeld. 1981. Econometric models and economic forecasts. McGraw-Hill Book Co., N.Y., 630 p.
- Pooley, S. G. 1985. The hopelessness of the invisible hand: Small versus large fishing vessels in Hawaii. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, Admin. Rep. H-85-2, 16 p.

- _____. Unpub. Competitive markets and bilateral exchanges: The wholesale seafood market in Hawaii. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.
- Ralston, S. 1979. A description of the bottom fish fisheries of Hawaii, American Samoa, Guam, and the Northern Marianas. A report submitted to the Western Pacific Regional Fishery Management Council, January 1979, 102 p.
- Samples, K. C., J. N. Kusakabe, and J. T. Sproul. 1984. A description and economic appraisal of charter boat fishing in Hawaii. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, Admin. Rep. H-84-6C, 130 p.
- Takenaka, B., L. Torricer, J. C. Cooper, and S. G. Pooley. 1984. Trends in the market for mahimahi and ono in Hawaii. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396, Admin. Rep. H-84-9, 20 p.
- [U.S.] National Marine Fisheries Service. 1985. Fisheries of the United States. Current Fishery Statistics No. 8360, 121 p.
- Vondruska, G., and F. Cunningham. 1985. Southeast finfish situation and outlook--1984. Southeast Region, Natl. Mar. Fish. Serv., NOAA, St. Petersburg, FL 33720, 16 p.
- Western Pacific Regional Fishery Management Council. 1985. Combined draft fishery management plan, environmental assessment and regulatory impact review for the bottom fish and seamount groundfish fisheries of the Western Pacific Region, var. pag.
- Wilson, J. A. 1980. Adaptation to uncertainty and small numbers exchange: The New England fresh fish market. Bell J. Econ. 11-2:491-504.

APPENDIX EQUATIONS

All equations involve logarithmic transformation of the continuous variables. The variables are also transformed to account for significant levels of serial correlation (determined by the Durbin-Watson test) through the Hildreth-Lu procedure (Pindyck and Rubinfeld 1981). The regression estimates are calculated using ordinary least squares techniques.

The results are given in the following form: The first line presents the equation number, a brief description, and the data source. The second line presents the dependent variable on the left and the independent variables on the right; the third line presents the beta coefficients of the regression; the fourth line presents the t-statistics; the fifth line presents summary information on the equation, including the coefficient of multiple determination (R^2), the resultant Durbin-Watson (DW) statistic for serial-correlation, the Hildreth-Lu serial-correlation correction factor (g), and the number of observations. Abbreviations for each variable are introduced below the equation. The quantity data are in pounds and prices by per pound. Statistical significance is represented by an asterisk (*), corresponding to a 95% confidence level.

All values are in natural logarithms except for the consumer dummy variable.

Equation 1: Hawaii bottom fish demand--1984 weekly wholesale data

PBTM	=	CNST	QBTM	CD
Beta		3.24	-0.23	0.42
t-statistic		-4.73*	5.14*	

$R^2 = 48.5\%$, $DW = 1.93$, $g = 0.2$, $N = 51$

BTTM:	The average price per pound of bottom fish, natural logarithms
QBBTM:	The average quantity of bottom fish sold in pounds per period, natural logarithms
CNST:	The constant
CD:	A consumer dummy variable taking the value of 1 for the high demand season and the value of 0 for the low demand season

*Significant at the 95% confidence level.

Equation 2: Hawaii bottom fish demand--1984 monthly wholesale data

PBTTM	=	CNST	QBTTM	CD
Beta		5.68	-0.42	1.04
t-statistic			-3.33*	2.21

$R^2 = 55.9\%$, $DW = 2.07$, $g = 0.8$, $N = 12$

Equation 3: Hawaii bottom fish demand by source of supply--pooled 1984 MHI and NWHI weekly data

PB:N:M	=	CNST	QBTTM	QN:Q	CD	M:N:S
Beta		2.62	-0.20	0.34	0.29	0.36
t-statistic			-4.00*	2.91*	4.29*	6.92*

$R^2 = 45.3\%$, $DW = 1.88^*$, $g = 0$, $N = 104$

PB:M:N: Average weekly price of bottom fish landed either from the MHI or NWHI, natural log
 QN:Q: Ratio of NWHI landings to total landings for the week
 M:N:S: A dummy variable valued 1 for MHI landings and 0 for NWHI landings

Equation 4: Hawaii bottom fish demand by group--1984 weekly wholesale data

PBTTM	=	CNST	QBTTMG1	QBTTMG2	QBTTMG3	CD
Beta		2.99	-0.13	-0.13	0.04	0.35
t-statistic			-3.30*	-2.90*	0.97	4.11*

$R^2 = 54.5\%$, $DW = 1.91^*$, $g = 0.2$, $N = 50$

QBTTMG1: Quantity for bottom fish group 1 (uku and ulua), natural log (equivalently for other groups)

Equation 5: Hawaii bottom fish demand group 1 (ulua and uku)--1984 weekly wholesale data

PBTTMG1	=	CNST	QBTTMG1	CD
Beta		1.52	-0.11	0.47
t-statistic			-1.64	3.87*

$R^2 = 30.9\%$, $DW = 1.84^*$, $g = 0$, $N = 52$

Equation 6: Hawaii bottom fish demand group 2 (opakapaka, et al.)--1984 weekly wholesale data

PBTTMG2	=	CNST	QBTTMG2	CD
Beta		3.04	-0.22	0.41
t-statistic			-6.19*	6.06*

$R^2 = 57.5\%$, $DW = 1.77^*$, $g = 0$, $N = 52$

Equation 7: Hawaii bottom fish demand group 3 (onaga, et al.)--1984 weekly wholesale data

PBTTMG3	=	CNST	QBTTMG2	CD
Beta		3.31	-0.11	0.31
t-statistic			-3.48*	1.96

$R^2 = 29.8\%$, $DW = 1.96^*$, $g = 0.6$, $N = 52$

Equation 8: Hawaii bottom fish group 1 (ulua and uku) cross effects--1984 weekly wholesale data

PBTTMG1	=	CNST	QBTTMG1	QBTTM2&3	CD
Beta		2.98	-0.08	-0.18	0.54
t-statistic			-1.25	-2.85*	4.70*

$R^2 = 40.9\%$, $DW = 2.17^*$, $g = 0$, $N = 52$

QBTTM2&3: Quantity for groups 2 and 3 combined, natural log (equivalently for other groups)

Equation 9: Hawaii bottom fish group 2 (opakapaka, et al.) cross effects--1984 weekly wholesale data

PBTMG2	=	CNST	QBTTMG2	QBTTM1&3	CD
Beta		3.43	-0.19	-0.08	0.39
t-statistic			-4.36*	-1.26	5.77*

$R^2 = 57.5\%$, $DW = 1.75^*$, $g = 0$, $N = 52$

Equation 10: Hawaii bottom fish group 3 (onaga, et al.) cross effects--1984 weekly wholesale data

PBTMG3	=	CNST	QBTTMG3	QBTTM1&2	CD
Beta		3.58	-0.10	-0.03	0.32
t-statistic			-2.65*	-0.53	1.97

$R^2 = 23.9\%$, $DW = 2.03^*$, $g = 0.6$, $N = 50$

Equation 11: Hawaii bottom fish demand by source--1984 weekly wholesale data

PBTM84	=	CNST	QMHI	QNWHI	CD
Beta		2.12	-0.10	-0.03	0.43
t-statistic			-2.04*	-0.88	4.08*

$R^2 = 32.9\%$, $DW = 2.02$, $g = 0.2$, $N = 47$

QMHI: Quantity landed from main Hawaiian Islands, natural log
 QNWHI: Quantity landed from Northwestern Hawaiian Islands, natural log

Equation 12: Main Hawaiian Islands bottom fish prices--
1984 weekly wholesale data

PMHI	=	CONST	QMHI	QNWHI	CD
Beta		2.29	-0.16	0.03	0.38
t-statistic			-3.43*	1.21	3.84*

$R^2 = 15.53\%$, $DW = 1.98^*$, $g = 0.2$, $N = 44$

PMHI: Average price for bottom fish landed from
the main Hawaiian Islands, natural log

Equation 13: Hawaii commercial landings, bottom fish
demand--HDAR monthly data, 1965-1982 (prices
adjusted by the December 1982 consumer price
index for Honolulu)

PBTTM[R]	=	CNST	RES	RDINC	QBTTM	CD
Beta		-9.29	1.56	0.05	-0.23	0.145
t-statistic			11.30*	0.67	-8.45*	4.25*

$R^2 = 44.9\%$, $DW = 2.12$, $g = 0.4$, $N = 214$

PBTTM[R]: Inflation-adjusted price of bottom fish,
natural log

QBTTM: Quantity of bottom fish (1,000s lb), natural
log

RES: Resident population in Hawaii (1,000s),
natural log

RDINC: Real disposable income per capita in Hawaii,
(inflation-adjusted), natural log

Equation 14: Hawaii commercial landings, cross effects--
HDAR monthly data, 1965-1982 (prices
adjusted by the December 1982 consumer price
index for Honolulu)

PBTM[R] =	CNST	QBTM	QTUNA	QMAHI	CD
Beta	1.78	-0.18	-0.13	0.13	0.12
t-statistic		-5.98*	-7.02*	6.65*	3.03*

$R^2 = 33.5\%$, $DW = 1.88^*$, $g = 0.4$, $N = 214$

QTUNA: Quantity of fresh market tuna (1,000s lb),
natural log

QMAHI: Quantity of mahimahi and wahoo (1,000s lb),
natural log

Equation 15: Hawaii bottom fish price trends--HDAR
monthly data, 1965-1982 (prices adjusted by
the December 1982 consumer price index for
Honolulu)

PBTM[R] =	CNST	PFISH[R]
Beta	0.71	0.29
t-statistic		8.85*

$R^2 = 25.7\%$, $DW = 2.08^*$, $g = 0.4$, $N = 214$

PFISH[R]: Price of all species, inflation-adjusted,
natural log

Mortality Rates of Snappers and Groupers

Stephen Ralston

Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
Honolulu, Hawaii 96822-2396

ABSTRACT

Mortality concepts are briefly reviewed and general methods of estimating mortality rates discussed. Special attention is devoted to techniques used successfully in the study of snappers and groupers. In particular, catch curves, Z/K ratio estimates, and the Pauly equation are shown to account for the majority of mortality estimates reported from these two taxa. A review of the snapper and grouper literature indicates that instantaneous rates of natural mortality (M) can simply be predicted with knowledge of the von Bertalanffy growth coefficient (K)--the former being roughly twice the latter. Reported agents responsible for natural deaths in these groups include predation, parasitism, cold water shock, and red tide poisoning. Examining levels of exploitation suggests that snappers have been more intensively harvested than groupers, although stocks characterized by high ratios of fishing to natural mortality are known from both families. Based on the evidence reviewed it is concluded that these species have a relatively limited productive capacity and are vulnerable to overfishing.

INTRODUCTION

In the tropical and subtropical waters of the world, few demersal fishery resources are more important than the snappers (Lutjanidae) and groupers (subfamily Epinephelinae of the Serranidae) (Bullis and Jones 1976; Pauly 1979;

Munro 1983). Yet in spite of their significance, yield assessments of these species have until recently been few (e.g., Ralston and Polovina 1982; Huntsman et al. 1983; Kunzel et al. 1983; Munro 1983; Powers 1983). Now, however, regional studies of snapper and grouper biology have proliferated to the extent that a review and synthesis of the information recently gained could considerably aid their management.

Estimation of mortality rates is central to demographic analyses and most types of stock assessment (Gulland 1955). This is because losses from exploited populations largely control the yields that can be obtained from them (Beverton and Holt 1957; Gulland 1971; Ricker 1975). Yet, biologists frequently regard the topic with apprehension because of preconceived ideas about its complexity. In truth, mortality concepts are quite simple, although statistical problems often do occur.

The organization of this chapter is, therefore, designed to first introduce several basic concepts which define what mortality is and in general terms how it is expressed mathematically. This leads to a discussion of specific methods and techniques for estimating mortality rates, especially those that have been successfully applied to snappers and groupers in tropical systems. Because natural mortality is of special significance when analyzing potential yield, and is usually difficult to determine, I present a brief discussion of factors correlating with it. From these ideas I develop a predictor of natural mortality and test it on data obtained from the snapper/grouper literature. This is followed by a review of factors known to be responsible for natural deaths in these two taxa. Finally, I briefly discuss the relationship between natural mortality and optimum rates of fishing mortality.

MORTALITY AND ITS ESTIMATION

When considered from the classical perspective of the Beverton and Holt (1957) dynamic pool model, there are three factors that uniquely determine the yield from a stock of fish. These factors are recruitment, growth, and mortality. The first two are renewal processes, which add biomass to the exploitable phase of the life history. Conversely, mortality represents the loss of individuals, and thus biomass, from the population. This loss process is usually subdivided into two separate categories:

deaths attributable to fishing, and deaths due to all other sources. Collectively the latter are termed natural mortality.

Jensen (1939) was among the first to argue that the force of mortality factors acts in a multiplicative fashion. He showed for a variety of stocks (including cod, haddock, plaice, and herring) that the number of individuals in a cohort or year class is diminished by a fixed percentage from year to year. Similarly, Beverton and Holt (1959) presented evidence for long-lived species demonstrating that a constant fraction of a cohort is removed each year by the various agents of natural mortality. Moreover, we know that when basic operational and statistical assumptions have been met, a fixed amount of fishing effort removes a fixed fraction of the fully vulnerable portion of a stock (Ricker 1975). Thus, at least in theory, fishing mortality operates in a multiplicative manner as well. In practice this may not be true.

The multiplicative nature of mortality factors lends itself to expression by the exponential function, especially in its differential form. Then the instantaneous total mortality rate from all causes (Z) can simply be defined as the proportionality constant that relates the rate of change (dN/dt) of a cohort to its absolute abundance (N). That is,

$$dN/dt = -ZN$$

It is a great convenience that, when mortality is expressed in this manner, fishing (F) and natural (M) mortality rates are additive; that is, $Z = F + M$. A necessary corollary is that total mortality equals natural mortality in the absence of fishing. When acting in concert, M and F compete for the individuals remaining in a year class, each responsible for a certain percentage reduction over time. Instantaneous mortality rates, as shown above, are by definition measured in units of inverse time, most frequently per year.

Given that mortality factors are related and expressed in this fashion, what methods are available to estimate these rates? Although a wide variety of techniques have been employed, most can be classified according to three fundamental types of estimation: (1) age-specific procedures for true cohorts; (2) time-specific methods for synthetic cohorts; and (3) mark-recapture methods. A very brief description of each follows.

Ideally, the total mortality rate of a cohort is estimated by determining the number of individuals of age x that are alive at time t , that is, $(N_{x,t})$, and also the number of individuals of age $x+1$ at time $t+1$ ($N_{x+1,t+1}$). If time is measured in years, the ratio of the latter to the former provides an estimate of the annual survivorship fraction (S_x) for fish aged x . Furthermore, the age-specific total instantaneous mortality rate (Z_x) is equal to $-\ln(S_x)$. Note that in this calculation an actual cohort is tracked in time and successively sampled. Thus, the measured mortality rate is the actual rate experienced by the cohort (Gulland 1955). An important practical adjustment often employed is to substitute properly subscripted catch per unit effort indices of abundance for the actual numbers of fish (Gray 1979; Paloheimo 1980; but see Butler and McDonald 1979). Age-specific mortality estimates are typically used in cohort and virtual population analysis (Ricker 1975) and result in the most compelling mortality assessments.

A second approach to the problem is through the use of synthetic cohorts. Rather than repetitively sampling a population through time, a single sample is taken and the numbers of fish aged x , $x+1$, $x+2$, ..., $x+i$ determined. Often this entails developing an age-length key (Fridriksson 1934; Gulland 1955), a nontrivial problem in its own right, especially if the key is used on samples taken at different times or places (Kimura 1977; Westrheim and Ricker 1978; Clark 1981). If the sampled population is assumed to be age-stationary (i.e., the age distribution remains the same from year to year), one can estimate mortality rates by forming the ratios of successive age classes exactly in the manner outlined previously. Note that computing mortality rates from "synthetic" cohorts actually produces estimates that are time-specific, as opposed to age-specific.

To analyze these kinds of data, Chapman and Robson (1960) and Robson and Chapman (1961) derived a minimum-variance, unbiased estimator of S for single age-frequency distributions in the situation where mortality rate is uniform across all age groups. Alternatively, the analysis of catch or survivorship curves (Ricker 1975) permits visual inspection of the data to look for possible violations of assumptions, especially that of constant mortality rate. These are simply semi-logarithmic plots of abundance against age, where the slope of the descending right-hand limb provides an estimate of total mortality rate. An important variation on this theme is

the analysis of single length-frequency distributions to estimate the ratio of total mortality rate to von Bertalanffy growth coefficient (Z/K) (Beverton and Holt 1956; Ssentongo and Larkin 1973; Powell 1979; Wetherall et al. In press). With an independent estimate of K from the study of tag returns, otoliths, modal size progression, etc., it is possible to estimate Z by separating the ratio. Similarly, there are techniques that assume an underlying growth structure, which is then used to analyze length-frequency distributions. These methods produce mortality estimates after analytically reconstructing the unknown age-distribution (Olsen and LaPlace 1979; Pauly 1982; see also Schnute and Fournier 1980). Although all these various techniques are commonly used, each relies essentially on a single sample, be it age- or length-frequency, and each therefore suffers from the constraint of age stationarity, an assumption that frequently is not met.

A third class of mortality estimation techniques involves mark-recapture methods (Ricker 1975; Seber 1982). For example, it is generally possible to estimate exploitation fraction ($u = 1 - \exp^{-F}$) in a marked population as the ratio of total marks in the catch to total marks in the population. From this, an estimate of fishing mortality is obtained directly. Similarly, total mortality rate can be estimated by determining the extinction rate of marks in the population at large. Other fairly detailed methods exist to estimate M . Mark-recapture methods have not been used, however, to estimate mortality rates of snappers and groupers.

While these three general categories account for the majority of mortality estimations, several other techniques have been developed that differ from them sufficiently to warrant specific mention. Green (1970), and later Ebert (1973), presented a method for estimating growth and total mortality rates by graphical and numerical means, respectively. Their method is restrictive in assuming age stationarity and full recruitment to the population over less than 1 month, but is appealing because it only requires estimates of average individual size at two times in the year. Saila and Lough (1981) derived an analytical solution to the same problem for an estimate of K , using this result in conjunction with the Z/K ratio method to separate the parameters. In yet another approach, Marten (1978) developed a procedure for determining total mortality rate from a length sample under conditions where fish growth can be considered

linear over the size range of interest. Also, regression analysis has been used effectively to separate Z into its constituent components (Beverton and Holt 1957; Cushing 1968). Here total mortality can be regressed against nominal fishing effort, in which case the y-intercept provides an estimate of M (see also Marten 1978). Similarly, Csirke and Caddy (1983) have suggested that a parabolic nonlinear regression of yield on total mortality rate (Z) allows estimation of M as the point of the left hand or ascending x-intercept.

Another means of estimating mortality, particularly natural mortality, is by comparative life history studies of ecologically or taxonomically similar species (Adams 1980; Gunderson 1980). For example, Pauly (1980) suggests predicting instantaneous natural mortality rate from a multiple regression equation he derived from the study of 175 fish stocks. This equation incorporates three independent variables: (1) mean annual water temperature; (2) the von Bertalanffy growth coefficient K ; and (3) either the asymptotic weight or length parameter from the von Bertalanffy growth model. Although the standard error of the estimate (0.247) is too large to permit precise estimation of natural mortality (estimated values of M have sometimes exceeded measured values of Z), this equation is still very useful when no historical information exists concerning the condition of a population in its unexploited state. Similarly, Hoenig (1983) presented an empirically derived equation which predicts total mortality rate from maximum age data.

MORTALITY ESTIMATION IN TROPICAL SNAPPERS AND GROUPERS

The only study of a snapper species in which age-specific mortality rates were determined for use in a cohort or virtual population analysis was that of Mahmoudi et al. (1984). The total catch of Rhomboplites aurorubens by age class, determined over a 10-year period, was estimated from size composition and total catch data from three distinct segments of the fishery (recreational, commercial hook-and-line, and commercial trawl). The data were aggregated and then recursively analyzed to obtain least squares estimates of age-specific fishing mortality rates from 1973 to 1982. Natural mortality was estimated from the Pauly (1980) equation. Given estimates of age-specific fishing mortality and catch it was possible to estimate the annual standing stock by age class and

recruit year-class strength. A graph relating the number of spawning females and recruitment was also presented. Thus a full history of the fishery was derived and a detailed assessment of the stock's response to exploitation was gained. They concluded that an increase in yield per recruit could be achieved by reducing fishing mortality on fish aged 1-3 years.

Without question catch curve analysis has been used more frequently on lutjanids and serranids than any other method of mortality estimation (Moe 1969; Manooch and Haimovici 1978; Nagelkerken 1979; Low 1981; Ivo and Hanson 1982; Nelson and Manooch 1982; Brouard and Grandperrin 1984; Matheson and Huntsman 1984; Moore and Labisky 1984; Ralston 1984; Witzig and Huntsman 1984). Studies have involved the following species: Epinephelus morio, E. cruentatus, E. niveatus, E. drummondhayi, Mycteroperca microlepis, Centropristis striata, Lutjanus purpureus, L. malabaricus, L. campechanus, Etelis carbunculus, E. coruscans, Pristipomoides flavipinnis, P. filamentosus, and P. multidentis. Typically, investigators have used hard parts, sometimes scales but more often otoliths, to develop a von Bertalanffy growth curve (see Manooch 1986).

Age-length data have usually been used to construct age-length keys, although some investigators have developed an age sample which is sufficiently large to permit analysis of population age structure directly (Moe 1969; Nagelkerken 1979; Low 1981). Otherwise, the use of age-length keys has been widespread, a practice that can result in seriously biased mortality estimates. Kimura (1977) and Westrheim and Ricker (1978) have both shown that a key derived from one population that is applied to another, or even if applied to the same stock sampled at different times, can produce substantial errors. This is because a single key used on divergent length-frequency data sets results in projected age distributions that tend to mimic the age distribution from which the key was derived. Misapplication of this method is therefore likely if the same key is used repeatedly. Consequently, when mortality estimates appear to remain uniform through time (e.g., Nelson and Manooch 1982; Witzig and Huntsman 1984), it is difficult to conclude that no change has occurred if only one age-length key was used. Clark (1981), however, has proposed a method to circumvent this problem, employing least squares to determine the overall age distribution of the population given the distribution of lengths within each age class (see also Bartoo and Parker 1983).

Another popular technique that can lead to error in mortality estimates is that of directly transforming lengths to ages using the inverse form of the von Bertalanffy growth equation (e.g., Mahmoudi et al. 1984). Age-frequency distributions developed in this fashion need not represent the actual age structure of the population (Ricker 1975; Bartoo and Parker 1983). When the data resulting from this procedure are analyzed by catch curve methods or otherwise, mortality estimates are likely to be biased.

At least two studies have used a modified catch curve approach. Pauly and Ingles (1982) estimated the total mortality rate of Epinephelus sexfasciatus using ELEFAN I (Pauly 1982), a computer program that generates length-converted catch curves from length-frequency data. Olsen and LaPlace (1979) also estimated total mortality rate in E. striatus by first restructuring length samples using probit analysis, and then deriving a probability function to estimate age class abundance by size class.

A method used extensively to estimate mortality rates, and apparently with great success, is the Z/K ratio technique and its subsequent modifications (Beverton and Holt 1956; Powell 1979; Wetherall et al. In press). In its simplest form, this method calculates the ratio of mortality to growth parameters from a length-frequency distribution adjusted to provide: (1) the size at which fish become fully vulnerable to the gear (l_c), and (2) the mean size of fish in the catch larger than l_c . It is attractive for its simplicity of data requirements and robustness of estimates (Powell 1979; Wetherall et al. In press; but see Majkowski 1982).

Several researchers have estimated mortality with this technique. Thompson and Munro (1978) computed Z for five species of Jamaican grouper: E. guttatus, E. striatus, M. venenosa, Cephalopholis fulva, and Petrometopon cruentatum. Because some length-frequency samples were obtained from unfished areas, they were also able to estimate natural mortality (i.e., $Z = M$). Brouard and Grandperrin (1984) used the Z/K ratio approach to estimate total mortality rates (= natural mortality) for six lutjanids in Vanuatu: Etelis carbunculus, E. coruscans, L. malabaricus, Pristipomoides flavipinnis, P. filamentosus, and P. multidentis. By comparison, estimates calculated from this approach averaged 24% higher than synoptic catch curve estimates for the same species. Ralston and Williams (Unpub.) also performed Z/K analyses for the same species (excluding L. malabaricus), as well

as P. auricilla and P. zonatus sampled in the Mariana Archipelago. Because their samples typically came from virgin populations, estimates of M were derived.

Age-specific mortality estimates for L. purpureus and Plectropomus maculatus were derived by Ivo and Gesteira (1974) and Goeden (1977), respectively, although the mortality rate was effectively constant among age classes in the latter study. Similarly, Nagelkerken (1979) and Manooch and Haimovici (1978) reported nonlinear descending limbs in catch curve analyses of Epinephelus cruentatus and M. microlepis. As a result, neither study attempted to estimate mortality. In the three studies where grouper mortality rates have demonstrated clear age-specific variation, all showed an increase in age specific mortality rate with increasing age (i.e., an upwardly convex catch curve). This finding is in agreement with the suggestion of Cushing (1968) that the collective force of natural mortality among the smaller fishes is largely due to predation but is more the result of physiological events (e.g., senility) for the larger, predatory species like snappers and groupers.

Another important means of estimating natural mortality rate (M) in the snappers and groupers has been the Pauly (1980) equation, used by Pauly and Ingles (1982) on E. sexfasciatus, Nelson and Manooch (1982) on L. campechanus, Brouard and Grandperrin (1984) on the six species mentioned previously (Pauly equation estimates were 46% greater than comparable catch curve estimates), Matheson and Huntsman (1984) on E. niveatus and E. drummondhayi, and Ralston (1984) on Pristipomoides filamentosus (equation estimate was 45% greater than a catch curve estimate from an unfished stock).

The only other two methods that have been employed to estimate mortality in these two groups are the Robson and Chapman (1961) maximum likelihood estimator, used by Nelson and Manooch (1982) on L. campechanus, and a regression of total mortality rate (Z) on nominal fishing effort, used to estimate natural mortality in L. purpureus by Ivo and Gesteira (1974). In the former study, the Robson-Chapman estimator produced estimates approximately 8% greater than catch curve estimates from the same data.

From this brief review, it is evident that three methods have accounted for the great majority of snapper/grouper mortality estimations: catch curves, Z/K ratios, and Pauly equation estimates. In situations where more than one of these has been used (Brouard and Grandperrin 1984; Ralston 1984), the Pauly (1980) equation produced

estimates of M that were distinctly higher than catch curve estimates derived from virgin stocks, while Z/K ratio estimates lay midway between the two.

PREDICTING NATURAL MORTALITY

Estimating instantaneous natural mortality rate (M) is of special significance in fisheries research (Ricker 1975). Although it is one of the most difficult parameters in fisheries to estimate, virtually all age-structured yield models require it. Once obtained, however, its uses are multiple.

One particular application of natural mortality estimates is to estimate maximum sustained yield (MSY). Alverson and Pereyra (1969), based on the unpublished ideas of Gulland (1971) and an earlier Soviet study (Tiurin 1962), first proposed that at MSY the optimum level of fishing mortality (F_{opt}) could be directly estimated with the natural mortality rate. This particular conclusion applied not only to surplus-production models like the Graham-Schaefer formulation, but more loosely to the Beverton and Holt (1957) constant recruitment model as well (Gulland 1971). Saetersdal (1973) also advocated using M as a direct estimate of F_{opt} when assessing unexploited resources and catch statistics are unavailable. From these ideas a number of studies have estimated MSY by the following relationship:

$$MSY = 0.5 M B_0$$

where B_0 represents exploitable virgin biomass. Kunzel et al. (1983), for example, estimated MSY for the lutjanids of the Mahe Plateau, Seychelles using this relationship.

Francis (1974), Deriso (1982), and Beddington and Cooke (1983) examined the theoretical basis for this approximation and concluded that it should hold only in situations where recruitment is constant over stock sizes ranging from B_0 to $0.5 B_0$. They showed on a purely analytical basis that if an asymptotic form of spawner-recruit curve were applicable, then $F_{opt} < M$, whereas if a dome-shaped relationship were in effect, then $F_{opt} > M$. Furthermore, optimum fishing mortality relative to MSY was generally shown to be less than F_{opt} for yield/recruit analyses.

Because of the biological importance of natural mortality and its utility in yield assessment, a number of

studies have tried to determine factors that might correlate with M , allowing its prediction from some other more easily estimated statistic. Beverton and Holt (1959) tabulated values of asymptotic size, K , maximum age, and M , and showed that the von Bertalanffy growth rate parameter K correlates well with M . Cushing (1968) summarized these findings in the statement "a fish with a high growth rate dies young" and presented plots of M versus K for the clupeoidei, gadiformes, salmonoidei, and pleuronectoidei.

More recently, Adams (1980) and Gunderson (1980) used r-K selection theory (MacArthur and Wilson 1967) as a basis for developing predictors of natural mortality. They concluded that the von Bertalanffy growth coefficient and the gonadosomatic index, respectively, were best correlated with M , although in all cases their trial predictors (size at maturity, asymptotic size, maximum age, and age at maturity) agreed well with r-K selection theory. Myers and Doyle (1983), under the assumption that fish life histories are evolutionary stable strategies, also estimated M from growth rate, fecundity, energy expenditure per egg, age and size at maturity, and a value of surplus energy available. Indeed, the Pauly (1980) equation itself relies on values of K , asymptotic size, and mean annual water temperature to predict M .

Based on the presumption that K is a good predictor of M , a survey of the snapper/grouper literature was undertaken that was designed to locate populations in which the von Bertalanffy growth coefficient (K) and the natural mortality rate were jointly estimated. An added appeal of K as a predictor of M is that both are measured in identical units (per year). Moreover, asymptotic size and mean annual water temperature are typically correlated with K and provide little independent information regarding M (but see Pauly 1980).

To determine if a more taxon-specific compilation of K and M statistics would increase the precision of natural mortality rate predictions, studies that used the Pauly (1980) equation to estimate snapper/grouper M were excluded unless an independent estimate was also given. Nineteen snapper/grouper stocks were identified in which the two parameters were both estimated. Table 8.1 summarizes the findings, including recent studies of 15 populations not incorporated in Pauly's original work. Some discussion of these is warranted.

Brouard and Grandperrin (1984) reported on six lutjanid species from Vanuatu, estimating Z by two independent means: catch curve and Z/K ratio. Growth was

TABLE 8.1

Summary information on growth and natural mortality determinations in the snapper and grouper families

Species	K	M	Source
Lutjanidae			
<u>Etelis</u>	0.07	0.08	Brouard and Grandperrin 1984
<u>carbunculus</u>			
<u>E. coruscans</u>	0.13	0.12	Brouard and Grandperrin 1984
	0.16	0.36	Ralston and Williams Unpub.
<u>L. malabaricus</u>	0.31	0.42	Brouard and Grandperrin 1984
<u>L. purpureus</u>	0.09	0.35	Menezes and Gesteira 1974
			Ivo and Gesteira 1974
<u>Ocyurus chrysurus</u>	0.16	0.20	Piedra 1965
<u>Pristipomoides</u>	0.27	0.66	Ralston and Williams Unpub.
<u>auricilla</u>			
<u>P. filamentosus</u>	0.15	0.25	Ralston 1984
			Ralston and Miyamoto 1983
	0.22	0.55	Ralston and Williams Unpub.
	0.29	0.53	Brouard and Grandperrin 1984
<u>P. flavipinnis</u>	0.36	0.83	Brouard and Grandperrin 1984
<u>P. multidentis</u>	0.24	0.42	Brouard and Grandperrin 1984
	0.19	0.63	Ralston and Williams Unpub.
<u>P. zonatus</u>	0.20	0.53	Ralston and Williams Unpub.
Serranidae			
<u>Epinephelus</u>	0.24	0.68	Thompson and Munro 1978
<u>guttatus</u>			
<u>E. niveatus</u>	0.09	0.18	Moore and Labisky 1984
<u>E. striatus</u>	0.09	0.23	Thompson and Munro 1978
<u>Mycteroperca</u>	0.13	0.29	Thompson and Munro 1978
<u>venenosa</u>			
<u>Plectropomus</u>	0.13	0.30	Goeden 1977
<u>maculatus</u>			

estimated by total counts of daily otolith increments. Because exploitation was negligible, each calculation can be considered an independent estimate of M . The value given in the table is the average of these two estimates (see discussion above). Ralston and Williams (Unpub.) studied six lutjanids from the Marianas as well as P. multidens from Papua New Guinea. With the single exception of P. flavipinnis, all their estimates of total mortality could be considered equivalent to natural mortality because of low or nonexistent levels of fishing. However, one of the remaining species (Etelis carbunculus) was excluded due to an aberrant population structure. Growth rates were determined by numerical integration of daily otolith increments. Of the five serranid species studied by Thompson and Munro (1978), reasonably reliable growth curves were developed from modal progressions and hard parts for the three species listed in the table. They estimated the ratio of total mortality to growth from a number of areas, one of which could be considered virgin fishing grounds, and separated the ratio using their growth estimates. Where parameter estimates were specified as a range, the interval midpoint was used here. Although age-specific mortality rates were given by Goeden (1977, see above) for Plectropomus maculatus, survivorship from age 2 to 3 is used here because the remaining estimates are unaccountably low.

Natural mortality rate is then plotted against the von Bertalanffy growth rate parameter in Figure 8.1, where, not surprisingly, it is seen that M is positively correlated with K ($r = 0.82$). Closed symbols in the figure represent the 14 lutjanid stocks while the 5 open circles depict the serranids. Among the former, the circles are from the study of Brouard and Grandperrin (1984) in Vanuatu, the squares from Ralston and Williams' (Unpub.) work on Marianas stocks, and the triangles represent the remaining four investigations of snappers (Piedra 1965; Menezes and Gesteira 1974; Ivo and Gesteira 1974; Ralston 1984; Ralston and Miyamoto 1983).

Analysis of covariance was used to determine whether the data from snappers and groupers could be pooled. The results showed that no differences were evident in either slope ($P = 0.29$) or adjusted means ($P = 0.42$), although clearly the size of the grouper sample was small. The data were then pooled and analyzed by linear regression (solid line in figure), with the following result:

$$M = 0.0189 + 2.06 K$$

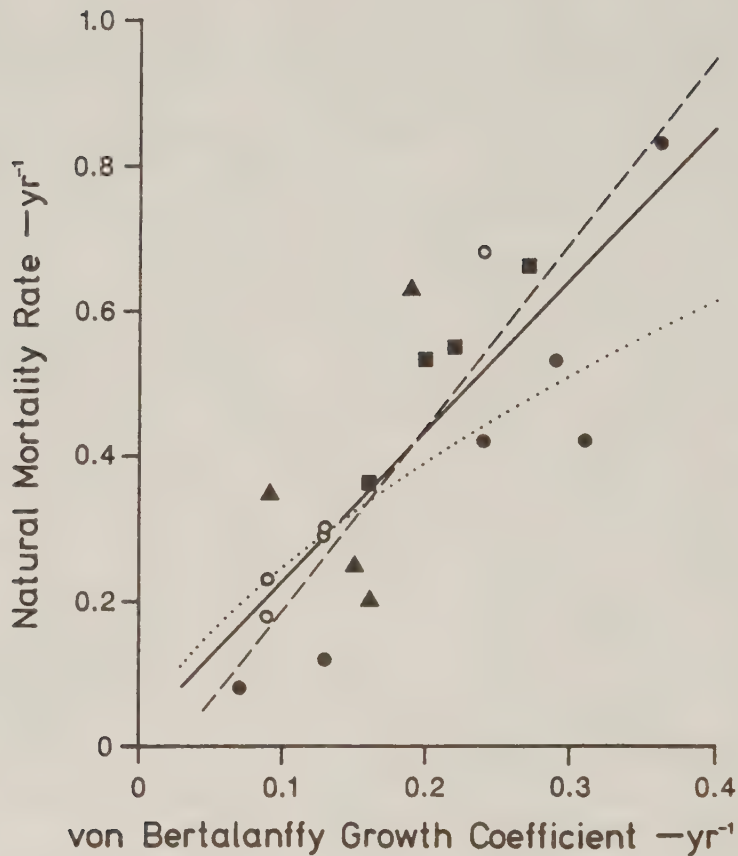


Figure 8.1 The relationship between natural mortality rate (M) and von Bertalanffy growth coefficient (K) for 19 stocks of snappers and groupers. See text for a detailed explanation of symbols

with standard errors for the intercept and slope equal to 0.0713 and 0.3528, respectively. The regression's slope was highly significant ($P < 0.0001$), although the estimate of intercept did not differ significantly from zero ($P = 0.79$). Thus, the ratio of natural mortality to growth rate within these two taxa is estimated to approximately 2, a simple rule of thumb that agrees with the data presented in Sylvester (1974). He presented length-frequency distributions for populations of L. vivanus, L. buccanella, and Pristipomoides macrophthalmus with negligible levels of exploitation, all of which had near linear descending (i.e., right-hand) limbs to the curves,

a characteristic of populations with mortality to growth ratios (Z/K) equal to 2 (Powell 1979). Similarly, highly skewed length-frequency distributions of L. campechanus (Bradley and Bryan 1975; Fable 1980) and Rhomboplites aurorubens (Fable 1980) are known from heavily exploited populations in which Z/K greatly exceeds 2.0.

The estimate of mean squared error for the regression in Figure 8.1 is 0.015, and thus the standard deviation of residuals is $s = 0.12$ per year. Although predictions of individual and population M values depend on specifying the level of K (Snedecor and Cochran 1967), one would expect the 95% confidence interval for a prediction to lie very roughly ± 0.24 per year above and below the regression line (i.e., two standard deviations). Similarly, approximately two-thirds of all observations are expected to lie within ± 0.12 per year of the regression.

Presented in the figure as a dashed line is the functional regression (Ricker 1973) of M on K , where:

$$M = -0.0666 + 2.52 K$$

Due to the nature of functional regressions, no statistical inference can be drawn from this result, except to say that it provides the best estimates of natural mortality rate if K is measured with a level of error comparable to that of M , a likely situation. If necessary, Ricker (1973) suggests using the symmetrical regression error limits obtained from the predictive analysis.

The dotted line in Figure 8.1 is the fit of a modified form of the Pauly (1980) equation to the data presented in Table 8.1. A simple $\log_{10}$ power function was made to pass through the means of $\log(K)$ and $\log(M)$, with the coefficient on the $\log_{10} K$ independent variable (0.665) obtained from the Pauly multiple regression equation. The result is to fit the data to his model, but using only one of the three variables he used. The graph shows that over the available range of K values the Pauly equation performs reasonably well, but tends toward overestimation of M for slow-growing species and underestimation of M for the faster growing ones.

The results presented here demonstrate that one can predict the natural mortality rate of snapper and grouper stocks with some accuracy, possessing nothing more than an estimate of the von Bertalanffy growth coefficient. These predictions are appreciably better than those calculated from the Pauly (1980) equation, both in terms of the distribution of residuals and the precision of estimates.

Comparable correlation coefficients were derived in the two studies (0.82 here versus 0.84 for Pauly's overall multiple correlation coefficient, and 0.58 for the second order partial correlation coefficient between M and K after the effects of temperature and asymptotic size were removed), although the range of available K values was 17 times greater in Pauly's study (0.04-4.92 per year). By necessity, residual variation must have correspondingly been reduced in Figure 8.1. Moreover, the standard deviation of $\log_{10}$ M values about the regression line (0.247) given in Pauly (1980) is indicative of a level of variation substantially greater than that in Figure 8.1 ($s = 0.12$ per year on untransformed M values). The improvement in predictive capability of the K variable is likely due to restricting the analysis to more narrowly defined taxa and habitats.

AGENTS OF NATURAL MORTALITY

A number of studies have reported incidental observations on factors actually or potentially responsible for the natural deaths of snappers and groupers. There have been four agents identified to date, including predation, parasitism, cold water shock, and red tides.

Starck and Schroeder (1970) were among the first to document predation on either of these groups, observing a great barracuda, Sphyraena barracuda, strike a gray snapper, L. griseus, and also finding the remains of another in the stomach of a cubera snapper, L. cyanopterus. Additionally, they also believed green morays, Gymnothorax funebris, were important predators of L. griseus. Bradley and Bryan (1975) found juvenile red snapper, L. campechanus, in the gut contents of a lizard fish, Synodontidae, and a dolphin, Coryphaena hippurus, and speculated that "sharks probably also prey on snappers." Likewise, Olsen and LaPlace (1979) observed sharks attacking Epinephelus striatus that had formed a breeding aggregation, and Fable (1980) saw amberjack, Seriola dumerili, and S. barracuda consume L. campechanus and R. aurorubens that had recently been tagged and released. From the available evidence it seems likely that predation related mortality on snappers and groupers is strongly size dependent, being most severe on the young.

Parasitism of lutjanids has been documented in several investigations (Starck and Schroeder 1970; Skinner 1982; Brusca and Gilligan 1983), but was apparently only a

serious problem where pollutants (ammonia, pesticides, etc.) so severely irritated and stressed a population of L. griseus that physical and physiological changes were induced, including epithelial hyperplasia, fusion of gill lamellae, and aneurisms. These changes resulted in reduced resistance to parasite infestations, which on occasion were debilitating (Skinner 1982).

Cold water shock has been cited repeatedly as a source of natural mortality in Florida's snappers and groupers. Starck and Schroeder (1970) reported that reduced water temperatures (11-14° C) resulting from cold snaps were known to kill L. griseus. Gilmore et al. (1978) observed mortality of E. itajara, E. morio, Mycteroperca microlepis, L. griseus, L. analis, and L. synagris from 13° C seawater. They also cite cold water intolerance by E. striatus, M. bonaci, Diplectrum formosum, L. apodus, L. jocu, and Ocyurus chrysurus. Likewise, Bohnsack (1983) observed E. striatus, L. apodus, and M. bonaci either dead or stunned from the effects of cold water (11-14° C) and concluded that "larger fish species and larger individuals within a species were the most sensitive to cold stress." Although in each of these studies thermal stress was cited as a major mortality factor, it is unlikely that most snappers and groupers, coming from more tropical climes, are similarly exposed to the threat of cold water shock.

The same is probably true of mass mortalities attributable to red tides, which typically are associated more with continental waters than insular areas. Smith (1976), however, documented extensive mortality in Gulf of Mexico populations of E. morio, E. itajara, M. microlepis, M. phenax, and L. griseus due to the effects of the red tide dinoflagellate Gymnodinium breve.

THE RELATIONSHIP OF FISHING MORTALITY TO NATURAL MORTALITY

As discussed previously, empirical and some theoretical justification exists to suppose that the optimum level of fishing mortality (F_{opt}) that can be applied to a stock to maximize biological yield is reasonably estimated by the natural mortality rate of the unfished population (Alverson and Pereyra 1969; Gulland 1971). Without detailed knowledge of the shape of the spawner-recruit relationship, however, it would seem more prudent to employ the range $0.8 M < F_{opt} < 1.5 M$ as reasonable bounds on an estimate of optimum fishing mortality (Francis 1974;

Deriso 1982; Beddington and Cooke 1983; Polovina 1986). Given this range for a target level of exploitation, what does the literature tell us about the intensity with which snapper/grouper stocks have been harvested?

A convenient means of expressing exploitation intensity is to scale fishing mortality by natural mortality, i.e., to form the ratio F/M . The ratio goes to zero in the absence of fishing and increases without bound as fishing mortality increases. An F/M ratio of 1.0 would correspond to the suggestion of Gulland (1971) that fishing mortality was at an optimal level. When properly scaled, comparisons become possible between stocks with differing mortality schedules and/or yield potentials.

The results presented in Table 8.2 provide a representative sampling of studies that have estimated snapper/grouper natural and fishing mortalities. The F/M ratio is presented for each, but some additional information is useful in interpreting the results.

The value for natural mortality used by Nelson and Manooch (1982) was obtained from the Pauly (1980) equation and equaled 0.20 per year. This estimate may be low since they estimated $K = 0.17$ per year. The relationship derived earlier would suggest that $M = 0.36$ per year may be a better estimate. If true, the F/M ratios listed for their study may be too high. The same is true of Matheson and Huntsman (1984), who used a Pauly estimate of $M = 0.20$ per year for E. drummondhayi when the von Bertalanffy growth rate parameter was determined to be $K = 0.13$ per year. For P. flavipinnis (Ralston and Williams Unpub.), the total mortality rate was determined by the Z/K regression method of Wetherall et al. (In press) and natural mortality from the relationship between K (0.20 per year) and M derived earlier. Although McErlean (1963) did not calculate the von Bertalanffy growth rate parameter or the mortality rate of M. microlepis, he presented information concerning both age at length and abundance in the catch by age class. These data were reanalyzed using a Walford plot and catch curve, respectively, yielding $K = 0.14$ per year and $Z = 1.20$ per year. Natural mortality was also estimated from the K of this species ($M = 0.30$ per year). One study that is not included is that of Moe (1969), because he estimated total mortality rate to be 0.32 per year with a K of 0.18 per year. These findings would suggest that the stock was lightly fished, even though it was believed to be heavily exploited for years.

The data from Table 8.2 were tabulated into a frequency distribution of F/M values, which is presented

TABLE 8.2

Summary information on the ratio of natural and fishing mortality estimates (F/M) for the snapper and grouper families

Species	F/M	Source
Lutjanidae		
<u>Lutjanus</u>	1.25	Nelson and Manooch 1982
<u> campechanus</u>	1.63	Nelson and Manooch 1982
	1.26	Nelson and Manooch 1982
	3.30	Nelson and Manooch 1982
<u>L. purpureus</u>	1.66	Ivo and Gesteira 1974
	1.94	Ivo and Hanson 1982
	2.23	Ivo and Hanson 1982
	1.73	Ivo and Hanson 1982
<u>Pristipomoides</u>	1.92	Ralston 1984
<u> filamentosus</u>		
<u>P. flavipinnis</u>	1.33	Ralston and Williams Unpub.
Serranidae		
<u>Centropristis</u>	1.77	Low 1981
<u> striata</u>	1.00	Low 1981
<u>Epinephelus</u>	0.85	Matheson and Huntsman 1984
<u> drummondhayi</u>	0.35	Matheson and Huntsman 1984
<u>E. guttatus</u>	0.28	Thompson and Munro 1978
	0.32	Thompson and Munro 1978
<u>E. niveatus</u>	0.27	Matheson 1981
	1.80	Matheson 1981
	1.93	Matheson and Huntsman 1984
	0.67	Matheson and Huntsman 1984
<u>E. sexfasciatus</u>	0.71	Pauly and Ingles 1982
<u>E. striatus</u>	2.52	Olson and LaPlace 1979
<u>Mycteroperca</u>	3.00	McErlean 1963 (recalculated)
<u> microlepis</u>		
<u>M. phenax</u>	2.00	Matheson et al. 1984
	1.24	Matheson et al. 1984

in Figure 8.2. Snapper stocks are shown in crosshatch and grouper populations are stippled. The solid line represents the frequency polygon for the combined snapper/grouper data.

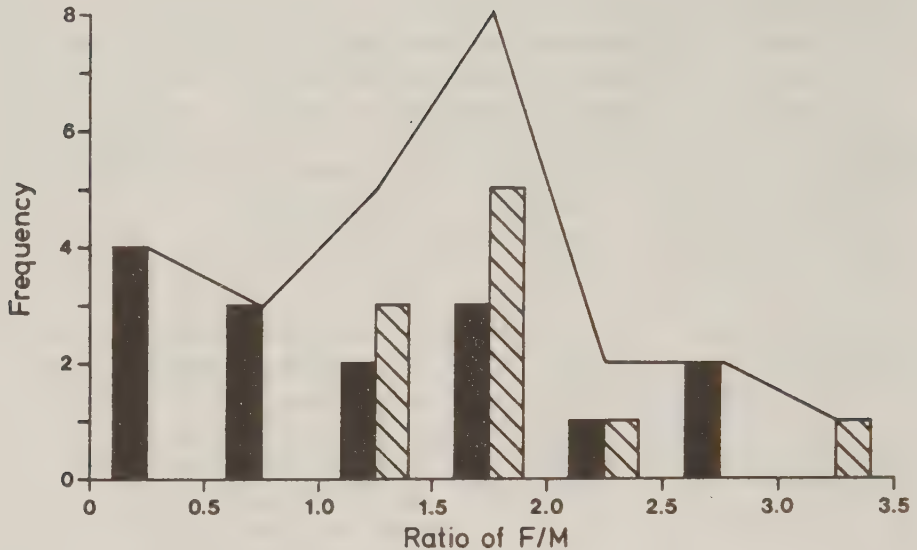


Figure 8.2 Exploitation intensity on snappers (crosshatch) and groupers (stipple). The figure presents the ratio of published values of fishing and natural mortality rates for 25 exploited stocks. The solid line represents the combined frequency polygon

At least two major trends are evident in the figure. It is clear that on a relative basis the lutjanid stocks reviewed here have been more intensely harvested than the groupers. Whether this conclusion is more generally warranted or whether it simply reflects a sampling or research bias is unknown. If, however, the pattern is real, it may reflect conservative fishing practices towards the epinephelines. This group is believed to be especially vulnerable to overexploitation, both because of their protogynous reproductive system and their tendency to aggregate during spawning (Johannes 1981; Shapiro 1986; but see Bannerot et al. 1986).

It is also apparent from the figure that many studies have determined fishing to natural mortality ratios far in excess of the 0.8 to 1.5 range suggested earlier. That some of these stocks are heavily exploited and have been so for years, is well documented (Camber 1955; Carpenter 1965; Ramirez 1970; Bradley and Bryan 1975; Tashiro and Coleman 1977). Nonetheless, the extreme levels of exploi-

tation that seem to characterize some snapper and grouper stocks (e.g., the Louisiana stock of L. campechanus cited by Nelson and Manooch (1982), where $F = 0.86$ per year and $F/M > 3.0$) are reason to assess the situation and develop alternative explanations for these data, including the following: (1) The theoretical basis for of the $F_{opt} = M$ approximation is in error; (2) the approximation is not applicable to snapper and grouper stocks; (3) the amount of replenishment or exchange between "stocks" is often so poorly understood that analyses of population dynamics tell us very little; and (4) some stocks are simply over-fished due to lack of management action.

With regard to relative levels of exploitation, one observation by Adams (1980) is particularly relevant. So-called "K" selected species are those with late maturity, slow growth rate, large asymptotic size, low rates of natural mortality, and extended maximum age. Note that K here refers to carrying capacity, which should not be confused with the von Bertalanffy growth coefficient. Members of the Lutjanidae and Epinephelinae, when placed on an r-K continuum defined by the community of tropical species with which they are found, tend to fit this description well (Beverton and Holt 1959; Pauly 1980). Simulation studies (Adams 1980) and actual fisheries experience (Huntsman et al. 1983; Mahmoudi et al. 1984) have shown that for these kinds of species, maximum yield per recruit (*sensu* Beverton and Holt 1957) is obtained at lower levels of fishing mortality and higher ages of recruitment (i.e., entry to the fishery) than their ecological counterparts. Furthermore, the relatively low levels of natural mortality that characterize snappers and groupers indicate a low natural turnover ratio (Allen 1971) and thus a reduced productive capacity (Alverson and Pereyra 1969; Gulland 1971). Fisheries for these kinds of species are also likely to develop excessive harvesting capacity during the fishing-up process (Francis 1984; Leaman and Beamish 1984). Based upon these considerations and on the high economic value of snappers and groupers, it is important that future efforts to manage these resources show caution and appropriate restraint.

BIBLIOGRAPHY

- Adams, P. B. 1980. Life history patterns in marine fishes and their consequences for fisheries management. Fish. Bull., U.S. 78:1-12.

- Allen, K. R. 1971. Relation between production and biomass. J. Fish. Res. Board Can. 28:1573-1581.
- Alverson, D. L., and W. T. Pereyra. 1969. Demersal fish explorations in the northwestern Pacific Ocean - An evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecasts. J. Fish. Res. Board Can. 26:1985-2001.
- Bannerot, S. P., W. W. Fox, Jr., and F. E. Powers. 1986. The biology and management of snappers and groupers in the tropics: Assessment and management in the Gulf of Mexico and Caribbean. In J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management. Westview Press, Inc., Boulder. [See this volume.]
- Bartoo, N. W., and K. R. Parker. 1983. Stochastic age-frequency estimation using the von Bertalanffy growth equation. Fish. Bull., U.S. 81:91-96.
- Beddington, J. R., and J. G. Cooke. 1983. The potential yield of fish stocks. FAO Fish. Tech. Pap. 242, 47 p.
- Beverton, R. J. H., and S. J. Holt. 1956. A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 140:67-83.
- _____. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. II. Mar. Fish., G. B. Minist. Agric. Fish. Food 19:1-533.
- _____. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. In G. E. Wolstenholme and M. O'Connor (editors), The lifespan of animals, p. 142-177. CIBA Found. Colloq. Aging 5.
- Bohnsack, J. A. 1983. Resiliency of reef fish communities in the Florida Keys following a January 1977 hypothermal fish kill. Environ. Biol. Fishes 9(1): 41-53.
- Bradley, E., and C. E. Bryan. 1975. Life history and fishery of the red snapper (Lutjanus campechanus) in the northwestern Gulf of Mexico: 1970-1974. Proc. 27th Annu. Gulf Caribb. Fish. Inst. p. 77-106.
- Brouard, F., and R. Grandperrin. 1984. Les poissons profonds de la pente recifale externe a Vanuatu. Notes et Documents d'Océanographie No. 11, 131 p. Mission ORSTOM, Port-Vila, Vanuatu.
- Brusca, R. C., and M. R. Gilligan. 1983. Tongue replacement in a marine fish (Lutjanus guttatus) by a

- parasitic isopod (Crustacea: Isopoda). *Copeia* 1983: 813-816.
- Bullis, H. R., Jr., and A. C. Jones, (editors). 1976. Proceedings: Colloquium on snapper-grouper fishery resources of the western central Atlantic Ocean. Fla. Sea Grant Coll. Rep. 17, 333 p.
- Butler, S. A., and L. L. McDonald. 1979. A simulation study of a catch-effort model for estimating mortality rates. *Trans. Am. Fish. Soc.* 108:353-357.
- Camber, C. I. 1955. A survey of the red snapper fishery of the Gulf of Mexico, with special reference to the Campeche Banks. Fla. Board Conserv. Mar. Res. Tech. Ser. 12, 64 p.
- Carpenter, J. S. 1965. A review of the Gulf of Mexico red snapper fishery. U.S. Fish Wildl. Serv., Circ. 208, 35 p.
- Chapman, D. G., and D. S. Robson. 1960. The analysis of a catch curve. *Biometrics* 16:354-368.
- Clark, W. G. 1981. Restricted least-squares estimates of age composition from length composition. *Can. J. Fish. Aquat. Sci.* 38:297-307.
- Csirke, J., and J. F. Caddy. 1983. Production modeling using mortality estimates. *Can. J. Fish. Aquat. Sci.* 40:43-51.
- Cushing, D. H. 1968. Fisheries biology, a study in population dynamics. University of Wisconsin Press, Madison, 200 p.
- Deriso, R. B. 1982. Relationship of fishing mortality and growth at the level of maximum sustainable yield. *Can. J. Fish. Aquat. Sci.* 39:1054-1058.
- Ebert, T. A. 1973. Estimating growth and mortality rates from size data. *Oecologia (Berl.)* 11:281-298.
- Fable, W. A., Jr. 1980. Tagging studies of red snapper (Lutjanus campechanus) and vermilion snapper (Rhomboplites aurorubens) off the south Texas coast. *Contrib. Mar. Sci.* 23(Aug.):115-121.
- Francis, R. C. 1974. Relationship of fishing mortality to natural mortality at the level of maximum sustainable yield under the logistic stock production model. *J. Fish. Res. Board Can.* 31:1539-1542.
- _____. 1984. Fisheries research and its application to west coast groundfish management. In T. L. Frady (editor), Proceedings of the Conference on Fisheries Management: Issues and Options, p. 285-304. Alaska Sea Grant Program, Fairbanks.
- Fridriksson, A. 1934. On the calculation of age distribution within a stock of cod by means of relatively

- few age-determinations as a key to measurements on a large scale. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 86:1-5.
- Gilmore, R. G., L. H. Bullock, and F. H. Berry. 1978. Hypothermal mortality in marine fishes off south-central Florida, January 1977. Northeast Gulf Sci. 2(2):77-97.
- Goeden, G. B. 1977. The life and loves of the coral trout. Aust. Fish. 36(8):16-18.
- Gray, D. F. 1979. Some extensions to the least squares approach to deriving mortality coefficients. Invest. Pesq. 43:241-243.
- Green, R. H. 1970. Graphical estimation of rates of mortality and growth. J. Fish. Res. Board Can. 27:204-208.
- Gulland, J. A. 1955. Estimation of growth and mortality in commercial fish populations. Fish. Invest. Ser., II Mar. Fish., G. B. Minist. Agric. Fish. Food 18(9):1-46.
- _____ (compiler and editor). 1971. The fish resources of the ocean. Fishing News (Books) Ltd., Surrey, Engl., 225 p.
- Gunderson, D. R. 1980. Using r-K selection theory to predict natural mortality. Can. J. Fish. Aquat. Sci. 37:2266-2271.
- Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull., U.S. 82:898-903.
- Huntsman, G. R., C. S. Manooch III, and C. B. Grimes. 1983. Yield per recruit models of some reef fishes of the U.S. South Atlantic Bight. Fish. Bull., U.S. 81:679-695.
- Ivo, C. T. C., and T. C. V. Gesteira. 1974. Estimacão preliminar das medidas de mortalidade do pargo Lutjanus purpureus Poey, no norte e nordeste Brasileiros. Arq. Cienc. Mar 14(2):123-127.
- Ivo, C. T. C., and A. J. Hanson. 1982. Aspectos da biologia e dinamica populacional do pargo, Lutjanus purpureus Poey, no norte e nordeste do Brasil. Arq. Cienc. Mar 22(1/2):1-41.
- Jensen, A. J. C. 1939. On the laws of decrease in fish stocks. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 110:86-96.
- Johannes, R. E. 1981. Words of the lagoon: Fishing and marine lore in the Palau District of Micronesia. University of California Press, Berkeley, 245 p.

- Kimura, D. K. 1977. Statistical assessment of the age-length key. *J. Fish. Res. Board Can.* 34:317-324.
- Kunzel, T., V. Lowenberg, and W. Weber. 1983. Demersal fish resources of the Mahe Plateau/Seychelles. *Arch. Fischereiwiss.* 34(1):1-22.
- Leaman, B. M., and R. J. Beamish. 1984. Ecological and management implications of longevity in some north-east Pacific groundfishes. *Int. North Pac. Fish. Comm. Bull.* 42:85-97.
- Low, R. A. Jr. 1981. Mortality rates and management strategies for black sea bass off the southeast coast of the United States. *N. Am. J. Fish. Manage.* 1:93-103.
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, 203 p.
- Mahmoudi, B., J. E. Powers, and G. R. Huntsman. 1984. Assessment of vermilion snapper of the northern South Atlantic Bight. Second Southeast Stock Assessment Workshop, June 4-8, 1984, Miami. Southeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, SAW/84/RFR/2, 36 p.
- Majkowski, J. 1982. Usefulness and applicability of sensitivity analysis in a multispecies approach to fisheries management. In D. Pauly and G. I. Murphy (editors), *Theory and management of tropical fisheries*, p. 149-165. Proceedings of the ICLARM/CSIRO Workshop on the Theory and Management of Tropical Multispecies Stocks, 12-21 January 1981, Cronulla, Australia. ICLARM Conf. Proc. 9.
- Manooch, C. S. III. 1986. A review of age and growth of the Lutjanidae and Serranidae. In J. J. Polovina and S. Ralston (editors), *Tropical snappers and groupers: Biology and fisheries management*. Westview Press, Inc., Boulder. [See this volume.]
- Manooch, C. S. III, and M. Haimovici. 1978. Age and growth of the gag, Mycteroperca microlepis, and size-age composition of the recreational catch off the southeastern United States. *Trans. Am. Fish. Soc.* 107:234-240.
- Marten, G. G. 1978. Calculating mortality rates and optimum yields from length samples. *J. Fish. Res. Board Can.* 35:197-201.
- Matheson, R. H. III. 1982. Age, growth, and mortality of two groupers, Epinephelus drummondhayi Goode and Bean and Epinephelus niveatus (Valenciennes), from North

- Carolina and South Carolina. M.S. Thesis, North Carolina State Univ., Raleigh, 67 p.
- Matheson, R. H. III., and G. R. Huntsman. 1984. Growth, mortality, and yield per recruit models for speckled hind and snowy grouper from the United States South Atlantic Bight. *Trans. Am. Fish. Soc.* 113:607-616.
- Matheson, R. H. III., G. R. Huntsman, and C. S. Manooch III. 1984. Age, growth, mortality, foods and reproduction of the scamp, Mycteroperca phenax, collected off North Carolina and South Carolina. Second Southeast Stock Assessment Workshop, June 4-8, 1984, Miami. Southeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, SAW/84/RFR/8, 38 p.
- McErlean, A. J. 1963. A study of the age and growth of the gag, Mycteroperca microlepis Goode and Bean (Pisces: Serranidae) on the west coast of Florida. *Fla. Board Conserv., Mar. Res. Lab. Tech. Ser.* 41: 1-29.
- Menezes, M. F. De., and T. C. V. Gesteira. 1974. Age and growth of the pargo, Lutjanus purpureus Poey, in northern and northeastern Brasil. *Arq. Cienc. Mar* 14(2):81-85.
- Moe, M. A., Jr. 1969. Biology of the red grouper Epinephelus morio (Valenciennes) from the eastern Gulf of Mexico. *Fla. Dep. Nat. Resour., Mar. Res. Lab. Prof. Pap. Ser.* 10:1-95.
- Moore, C. M., and R. F. Labisky. 1984. Population parameters of a relatively unexploited stock of snowy grouper in the lower Florida Keys. *Trans. Am. Fish. Soc.* 113:322-329.
- Munro, J. L. 1982. Estimation of biological and fishery parameters in coral reef fisheries. In D. Pauly and G. I. Murphy (editors), *Theory and management of tropical fisheries*, p. 71-82. Proceedings of the ICLARM/CSIRO Workshop on the Theory and Management of Tropical Multispecies Stocks, 12-21 January 1981, Cronulla, Australia. ICLARM Conf. Proc. 9.
- _____. (editor). 1983. Caribbean coral reef fishery resources. *ICLARM Stud. Rev.* 7, 276 p.
- Myers, R. A., and R. W. Doyle. 1983. Predicting natural mortality rates and reproduction--mortality trade-offs from fish life history data. *Can. J. Fish. Aquat. Sci.* 40:612-620.
- Nagelkerken, W. P. 1979. Biology of the graysby, Epinephelus cruentatus, of the coral reef of Curacao. *Stud. Fauna Curacao Other Caribb. Isl.* 60:1-118.

- Nelson, R. S., and C. S. Manooch III. 1982. Growth and mortality of red snappers in the west-central Atlantic Ocean and northern Gulf of Mexico. *Trans. Am. Fish. Soc.* 111:465-475.
- Olsen, D. A., and J. A. LaPlace. 1979. A study of a Virgin Islands grouper fishery based on a breeding aggregation. *Proc. 31st Annu. Gulf and Caribb. Fish Inst.*, p. 130-144.
- Paloheimo, J. E. 1980. Estimation of mortality rates in fish populations. *Trans. Am. Fish. Soc.* 109:378-386.
- Pauly, D. 1979. Theory and management of tropical multispecies stocks: A review with emphasis on the Southeast Asian demersal fisheries. *ICLARM Stud. Rev.* 1, Manila, 35 p.
- _____. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. Cons. Int. Explor. Mer* 39:175-192.
- _____. 1982. Studying single-species dynamics in a tropical multispecies context. In D. Pauly and G. I. Murphy (editors), *Theory and management of tropical fisheries*, p. 33-70. *Proceedings of the ICLARM/CSIRO Workshop on the Theory and Management of Tropical Multispecies Stocks*, 12-21 January 1981, Cronulla, Australia. *ICLARM Conf. Proc.* 9.
- Pauly, D., and J. Ingles. 1982. Aspects of the growth and natural mortality of exploited coral reef fishes. In E. D. Gomez, C. E. Birkeland, R. W. Buddemeir, R. E. Johannes, J. A. Marsh, Jr., and R. T. Tsuda (editors), *Proc. 4th Int. Coral Reef Symp.*, Manila, 1:89-98.
- Piedra, G. 1965. Materials on the biology of the yellow-tail snapper (*Ocyurus chrysurus* Bloch). In A. S. Bogdanov (editor), *Sovetsko-Kubinskie rybokhozyaistvennye issledovaniya. Izdatel'stvo "Pishchevaya Promyshlennost'."* [Soviet-Cuban Fish. Res.] (Transl. IPST 5514, TT 69-59016, p. 251-269. 1969. Clearinghouse Fed. Sci. Tech. Inf., Springfield, Va.)
- Polovina, J. J. 1986. Assessment and management of deepwater bottom fishes in Hawaii and the Marianas. In J. J. Polovina and S. Ralston (editors), *Tropical snappers and groupers: Biology and fisheries management*. Westview Press, Inc., Boulder. [See this volume.]
- Powell, D. G. 1979. Estimation of mortality and growth parameters from the length frequency of a catch. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer* 175:167-169.

- Powers, J. E. 1983. Report of the Southeast Fisheries Center stock assessment workshop August 3-6, 1982. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SEFC-127, 229 p.
- Ralston, S. 1984. Biological constraints on production and related management issues in the Hawaiian deepsea handline fishery. In R. W. Grigg and K. Y. Tanoue (editors), Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands, Vol. 2, May 25-27, 1983, Univ. Hawaii, Honolulu, p. 248-264. UNIHI-SEAGRANT-MR-84-01.
- Ralston, S., and G. T. Miyamoto. 1983. Analyzing the width of daily otolith increments to age the Hawaiian snapper, Pristipomoides filamentosus. Fish. Bull., U.S. 81:523-535.
- Ralston, S., and J. J. Polovina. 1982. A multispecies analysis of the commercial deep-sea handline fishery in Hawaii. Fish. Bull., U.S. 80:435-448.
- Ralston, S., and H. A. Williams. Unpub. Age, growth, and mortality of lutjanid and other deep slope fishes from the Mariana Archipelago. Southwest Fish. Cent., Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.
- Ramirez, M. S. 1970. The red grouper fishery of Yucatan Peninsula, Mexico. Proc. 22d Gulf Caribb. Fish. Inst., p. 122-129.
- Ricker, W. E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.
- _____. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.
- Robson, D. S., and D. G. Chapman. 1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90:181-189.
- Saetersdal, G. 1973. Assessment of unexploited resources. J. Fish. Res. Board Can. 30:2010-2016.
- Saila, S. B., and R. G. Lough. 1981. Mortality and growth estimation from size data - an application to some Atlantic herring larvae. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178:7-14.
- Schnute, J., and D. Fournier. 1980. A new approach to length-frequency analysis: Growth structure. Can. J. Fish. Aquat. Sci. 37:1337-1351.
- Seber, G. A. F. 1982. The estimation of animal abundance. MacMillan Publishing Co., Inc., N.Y., 654 p.

- Shapiro, D. Y. 1986. Reproduction in groupers. In J. J. Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management. Westview Press, Inc., Boulder. [See this volume.]
- Skinner, R. H. 1982. The interrelation of water quality, gill parasites, and gill pathology of some fishes from South Biscayne Bay, Florida. Fish. Bull., U.S. 80:269-280.
- Smith, G. B. 1976. The impact of fish-killing phytoplankton blooms upon mideastern Gulf of Mexico reef fish communities. In H. R. Bullis, Jr. and A. C. Jones (editors), Proceedings: Colloquium on Snapper-Grouper Fishery Resources of the Western Central Atlantic Ocean, p. 185-191. Texas A&M Univ. Sea Grant Coll. and Mississippi-Alabama Sea Grant Consortium. Fla. Sea Grant Coll. Rep. 17.
- Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. Iowa State Univ. Press, Ames, 593 p.
- Ssentongo, G. W., and P. A. Larkin. 1973. Some simple methods of estimating mortality rates of exploited fish populations. J. Fish. Res. Board Can. 30:695-698.
- Starck, W. A. II, and R. E. Schroeder. 1970. Investigations of the gray snapper, Lutjanus griseus. Stud. Trop. Oceanogr. (Miami) 10, 224 p., 44 figs. (Copyright 1971.)
- Sylvester, J. R. 1974. A preliminary study of the length composition, distribution, and relative abundance of three species of deepwater snappers from the Virgin Islands. J. Fish Biol. 6:43-49.
- Tashiro, J. E., and S. E. Coleman. 1977. The Cuban grouper and snapper fishery in the Gulf of Mexico. Mar. Fish. Rev. 39(10):1-6.
- Thompson, R., and J. L. Munro. 1978. Aspects of the biology and ecology of Caribbean reef fishes: Serranidae (hinds and groupers). J. Fish Biol. 12: 115-146.
- Tiurin, P. V. 1962. Factor estestvennoi smertnosti ryb i ego znachenie pri regulirovanii rybolovstva (The natural mortality factor and its importance in regulating fisheries). Vopr. Ikhtiol. 2:403-427. (Fish. Res. Board Can. Transl. Ser. 558).
- Westrheim, S. J., and W. E. Ricker. 1978. Bias in using an age-length key to estimate age-frequency distributions. J. Fish. Res. Board Can. 35:184-189.

- Wetherall, J. A., J. J. Polovina, and S. Ralston. In press. Estimating growth and mortality in steady state fish stocks from length-frequency data. In D. Pauly and G. R. Morgan (editors), Length-based methods in fishery research. The ICLARM/KISR Conference on the Theory and Application of Length-Based Methods for Stock Assessments, Sicily, Italy, February 1985. Vol. 1.
- Witzig, J. F., and G. R. Huntsman. 1984. Report: Mortality rates of South Atlantic reef fishes as determined from samples of the headboat fishery. Second Southeast Stock Assessment Workshop, June 4-8, 1984, Miami. Southeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, SAW/84/RFR/6, 24 p.

Reanalysis of Rate of Change in the California-Chukotka Gray Whale Stock, 1967/68 – 1979/80

S. B. Reilly

Southwest Fisheries Center, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038, USA

ABSTRACT

A statistical analysis of the relationships among annual population estimates, mean annual visibility and mean distance offshore of passing whales from the 1967-1980 Monterey gray whale censuses indicates that there was in fact a significant positive rate of change in gray whale abundance during those years.

INTRODUCTION

The rate of change in size of the eastern Pacific gray whale population during recent years is a topic of interest to both US and international resource management organizations. An earlier analysis of the 13 year consecutive shore census series from Monterey, California concluded that the population had shown a net positive rate of change of about 2.5% per year from 1967/8 through 1979/80. A survey of other time series of gray whale population indices (Reilly, 1984) concluded that these other data sources were less reliable.

In a subsequent, brief review of information relevant to the net recruitment rate of eastern Pacific gray whales, Cooke (1986) suggested that the significant increase of 2.5% per year was an artifact of a statistical confounding of population estimates with the mean estimated distance offshore of passing whales, which had not been taken into account in the original trend analysis (Reilly *et al.*, 1983). Cooke included in his analysis only data collected during the first 11 years of the Monterey series, as published in Reilly *et al.* (1980). The present study was undertaken to test Cooke's (1986) result, given the additional two consecutive years' data available.

In examining factors relevant to variation in the mean estimated distance offshore of passing whales, one must include sighting or visibility conditions. It is in keeping with both sighting theory and common sense that as visibility conditions worsen, more whales far from shore will be missed, and mean recorded distance will decrease. In this paper I report on a simple statistical examination of the relationships among the annual population estimates, estimated mean offshore distances and mean visibility conditions, and the time sequence of the estimates.

METHODS

The data analyzed here were from the US National Marine Mammal Laboratory's Monterey gray whale census data base. The procedures used and the variables recorded in the Monterey censuses were described in Reilly *et al.* (1980, 1983) for the years 1967-1980. The population estimates and their variances were also taken from Reilly *et al.* (1983).

Population estimates for the 1984/85 and 1985/86 Monterey censuses were not included in this analysis because they are not strictly comparable with the estimates for 1967/68 through 1979/80. In estimating total abundance from the actual counts Breiwick and Dahlheim (1986) did

not include correction for whales missed offshore. The offshore distances recorded in the later two censuses appeared to differ markedly from those recorded during the 13 year series from 1967/8 through 1979/80, so correction factors estimated during the earlier series were of questionable relevance.

The data used in this analysis were annual estimates of abundance, mean estimated offshore distance of passing whales and average sighting conditions. The annual average visibility codes and distance estimates were computed from data collected on 'good' visibility days. The data from 'poor' visibility days were excluded here from the computation of mean visibility and distance. This follows the population estimation procedure of Reilly *et al.* (1983) where the number of whales passing on 'poor' days was estimated from a gamma probability model (which had been previously fitted to the time sequence of daily counts) rather than from the raw data. That is, a day's count data were included here (in the computation of annual mean visibility and distance) if the average visibility code for the day was 4.0 or less, on a scale from 1 (excellent conditions) to 6 (very bad) following Reilly *et al.* (1983). Table 1 lists the annual population estimates, mean visibility and distance estimates (and accompanying statistics) used in the trend analysis.

Table 1

Annual population estimates (N), their std. deviations (sd(N)), mean visibility codes (V) recorded on 'good' visibility days (see text for definition), their std. errors (se(V)), mean estimated distances (D) of pods sighted on 'good' visibility days their std. errors (se(D)) and sequence number of the year (T). All statistics are from the Monterey gray whale censuses.

Year	N	sd(N)	V	se(V)	D	se(D)	T
1967/8	13095	1276	2.46	0.153	3.60	0.114	1
1968/9	11954	1545	2.28	0.170	0.45	0.082	2
1970/1	11177	1625	2.58	0.105	0.57	0.085	4
1971/2	10614	918	2.45	0.110	0.73	0.126	5
1972/3	14534	1348	2.63	0.103	0.67	0.099	6
1973/4	14676	1558	2.68	0.133	0.62	0.112	7
1974/5	13110	1366	2.32	0.136	0.82	0.144	8
1975/6	15919	1903	3.47	0.111	0.46	0.085	9
1976/7	16621	1798	2.73	0.113	0.41	0.066	10
1977/8	14811	2272	3.48	0.153	0.38	0.106	11
1978/9	13676	1127	2.14	0.122	0.73	0.107	12
1979/80	17577	2364	2.55	0.127	0.64	0.113	13

The basic method used to investigate trends in the population estimates with time was stepwise multiple regression. The correlation matrix is also presented (Table 2).

Table 2

Correlation matrix. N is annual population estimate, SD(N) is std. deviation of the N, V is mean visibility code recorded during 'good' visibility days, SE(V) its std. error, D is the mean estimate of offshore distance of counted pods, SE(D) its std. error, T is the year, with 1967/8 scaled as 1. * Significantly different from zero at $\alpha < 0.05$.

	N	SD(N)	V	SE(V)	D	SE(D)	T
N	1.000						
SD(N)	0.681*	1.000					
V	0.435	0.600*	1.000				
SE(V)	-0.164	0.172	-0.092	1.000			
D	-0.297	-0.600*	-0.667*	-0.293	1.000		
SE(D)	-0.215	-0.305	-0.322	0.093	0.778*	1.000	
T	0.719*	0.487	0.282	-0.343	0.027	0.076	1.00

Five simple models were examined: (1) annual population estimate (N) as the dependent variable in a simple linear model, with no weighting; (2) N, weighted by $1/\text{var}(N)$; and (3) an exponential model, made linear by transforming N to $\ln(N)$, with weights $N^2/\text{var}(N)$ (see Reilly *et al.*, 1983 for derivation). In these first three models, the following variables were available for inclusion in the predictor set: time (T, in years, with 1967/68 defined as 1), average annual visibility code (V), and average offshore distance of sighted pods (D). In the exponential models, $\ln(D)$ and $\ln(V)$ were used in place of D and V. Variables were selected for inclusion in the model if the alpha level was 0.05 or less from a test of the hypothesis that the variable's regression coefficient was equal to zero.

Model 4 was the same as model 2 except that D and V were included in the regression regardless of their contribution to model fit (i.e. forced), to examine the resultant slope of N on time. Model 5 was the same as model 3 except for the forced inclusion of $\ln(D)$ and $\ln(V)$.

RESULTS

Six variable correlations were significantly different from zero (Table 3). Two of these were correlations of estimates with their dispersion statistics (N with SD(N) and D with SE(D)), and were to be expected. The other four are noteworthy. There was a high, positive correlation of population estimate with time ($r = 0.72$), and no significant correlations of N with D or V. There was, however, a large negative correlation of V with D ($r = -0.67$), that is, as

visibility conditions became worse (the average code recorded increased) the mean estimated offshore distance decreased. There were also significant correlations of D and V with the standard deviation of the population estimates. Higher SD(N)s were associated with worse visibility conditions and mean distance estimates closer to shore.

Neither D nor V were included in a stepwise regression (Table 3) with N in the first three models, under a standard entry criterion of $\alpha < 0.05$. In the simple model (no. 4) where D and V were included in the regression there was a small increase in the estimated rate of increase in comparison to model 2 which included only N and T ($b = 344$ vs 313 whales per year, where b is the slope of the regression). In the exponential model where $\ln(D)$ and $\ln(V)$ were forced (no. 5) there was no change in the estimated rate of increase in relation to model 3, which did not include D and V.

DISCUSSION

Given the population estimates and variances from Reilly *et al.* (1983) we find a significant increase in population size indicated for the period 1967-1980, even when the annual mean visibility conditions and mean offshore distance estimates were taken into account. The significant negative correlation of offshore distance estimates and mean visibility conditions, along with the correlations of these variables with the standard deviation of the population estimates is understandable. As visibility conditions worsen, more whales far from shore are missed. This pattern remains even after discarding all data from days with poor average visibility conditions.

A higher mean visibility code on the 'good' days is almost certainly associated with more 'bad' days in a year. Also, there is a large variance contribution (in the abundance estimation procedure of Reilly *et al.*, 1983) from using the gamma model to estimate a day's number of whales passing rather than using the actual count. Thus a higher variance (or standard deviation) for an annual abundance estimate would be associated with a higher mean visibility code.

While the unweighted regression of N on T (model no. 1) resulted in a better fit to the data, the weighted models are

Table 3

Summary of stepwise multiple regressions of population estimates (N), on time (T), average estimated offshore distance of sighted pods (D) and average visibility code (V).

Model/ Depend. var.	Weight	Selection criterion	Variables included	B values	SE(B)	P(t)	Model F	P(F)
(1) N	none	0.05	intercept T	11,112.00 390.29	113.9	0.006	11.74	0.006
(2) N	1/ var(N)	0.05	intercept T	11,132.57 313.52	134.41	0.039	5.44	0.039
(3) $\ln(N)$	N^2 / var(N)	0.05	intercept T	9.3313 0.0251	0.0096	0.024	6.80	0.024
(4) N	1/ var(N)	force	intercept V D T	13,114.29 691.36 -6,240.38 344.06	1731.38 4691.97 125.36	0.699 0.216 0.023	3.81	0.052
(5) $\ln(N)$	N^2 / var(N)	force	intercept $\ln(V)$ $\ln(D)$ T	9.0354 0.2236 -0.1700 0.0253	0.3594 0.2139 0.0092	0.535 0.411 0.024	3.59	0.061

preferable, since they included the effect of a heterogeneous variance structure in the population estimates, and thus better met the assumptions of the regression model.

Given the lack of significant statistical association of annual mean distance and annual mean visibility statistics with the time trend of abundance estimates, there was no apparent reason to further consider (in this specific analysis) these factors, or the models into which they were forced. This does not imply that all possible effects on abundance estimation or trend analysis from variation in visibility conditions and offshore distance estimates have been considered and accounted for. Annual means may not contain sufficient information to fully reflect underlying processes.

The rates of increase estimated here were 2.29% per year (with 95% c.i. 0.33, 4.24) from the simple linear model weighted by the reciprocal of the variances (no. 2), and 2.51% per year (0.59, 4.43) from the weighted exponential model (no. 3). In both cases the coefficient of determination was somewhat low (0.33 and 0.38, respectively) and this was reflected in the broad confidence intervals. Model 3 reported here is the same model and results reported earlier in Reilly *et al.* (1983).

ACKNOWLEDGEMENTS

Thanks are due to Justin Cooke for suggesting this reanalysis, to Jeff Breiwick, Randall Peterman and Pierre

Kleiber for helpful discussions. Randall Peterman (Simon Fraser University, Burnaby, B.C. Canada), Douglas Chapman (University of Washington, Center for Quantitative Science, Seattle, WA USA), Daniel Goodman (Montana State University, Bozeman, Montana USA), Justin Cooke (University of York, Heslington, York, UK) and Jean Michalski (Southwest Fisheries Center) provided useful comments on the draft.

REFERENCES

- Breiwick, J.M and Dahlheim, M.E. 1986. Preliminary results from the 1985/86 gray whale census. Paper SC/38/PS14, presented to the IWC Scientific Committee, May 1986 (unpublished).
- Cooke, J. G. 1986. On the net recruitment rate of gray whales with reference to inter-specific comparisons. *Rep. int. Whal. Commn* 36: 363-6.
- Reilly, S.B. 1984. Observed and maximum rates of increase in gray whales, *Eschrichtius robustus*. *Rep. int. Whal. Commn* (special issue 6): 389-99.
- Reilly, S.B., Rice, D.W. and Wolman, A.A. 1980. Preliminary population estimate for the California gray whale based upon Monterey shore censuses, 1967-68 to 1978-79. *Rep. int. Whal. Commn* 30: 359-68.
- Reilly, S.B., Rice, D.W. and Wolman, A.A. 1983. Population assessment of the gray whale, *Eschrichtius robustus*, from California shore censuses, 1967-1980. *Fish. Bull. U.S.* 81(2): 267-81.
- Rugh, D., Ferrero, R. and Dahlheim, M. 1986. Inter-observer count discrepancies in a shorebased census of gray whales. Paper SC/38/PS15, presented to the IWC Scientific Committee, May 1986 (unpublished).

Patterns in Longline Fishery Data and Catches of Bigeye Tuna, *Thunnus obesus*

GARY T. SAKAGAWA, ATILIO L. COAN, and NORMAN W. BARTOO

Background

Longline gear has been an effective and traditional fishing gear used to catch large tunas in the open oceans. The method was perfected by the Japanese in the 1930's, but its use did not spread outside the Japanese archipelago until after World War II (Shapiro, 1948). Currently, Japan, Korea, and Taiwan have large, specialized fleets that use longlines for catching tunas in the major oceans and seas. As many as 2,000 longline vessels are engaged in fishing primarily for tunas.

The basic design of the longline gear, a long mainline suspended from floats to which branch lines with hooks are attached, is simple and generally uniform between vessels (Shingu et al., 1980). What is unusual is that the gear can be deployed in specialized ways to catch more of certain species than others. This characteristic was most recently shown for the Japanese fleet in the Pacific Ocean. Japanese scientists showed that

by removing intermediate floats from a standard longline gear, the mainline sags forming a deeper catenary so that the branch lines fish deeper. Fishermen were able to substantially improve their catch rates for bigeye tuna, *Thunnus obesus*, a preferred species, while reducing the catch rates for other tuna species (Suzuki et al., 1977). Other such techniques, e.g., night longlining for swordfish (Ueyanagi, 1974) have been described in the literature.

In this paper, we review available longline fishery statistics for the Japanese, Korean, and Taiwanese fleets for catch patterns. The patterns are then evaluated with respect to market information, which may have affected tuna fisheries (Suda, 1974; Ueyanagi, 1974; Lee, 1986; Wise and Miyake, 1982). Our emphasis is on the longline catch of bigeye tuna in the Atlantic, but we also review information on the catch of yellowfin tuna, *T. albacares*, and albacore, *T. alalunga*, from other oceans. We do not review, except in a discussion of global events, the catch of bluefin tunas, *T. thynnus* and *T. maccoyi*, because they are caught in specialized fisheries that are monopolized by the Japanese fleet.

The Longline Gear

Longline gear consists of a mainline with float lines and branch lines of baited hooks (Fig. 1). Float lines are attached to the mainline to regulate depth. This gear is deployed for tunas early in the morning and then retrieved, beginning around

noon and ending frequently after midnight (Ueyanagi, 1974). Each operation or set involves setting of 150-350 baskets (the mainline is coiled in baskets) of mainline, extending over a distance of 25-75 km, with about 2,000 baited hooks.

Standard longlining fishes at a maximum depth of around 170 m, with 4-6 branch lines per basket of mainline. Deep longlining, which was introduced in the Pacific and Indian Oceans in the early 1970's and in the Atlantic in 1978, fishes at a maximum depth of about 300 m with an average of 13 branch lines per basket (Suzuki et al., 1977). Deep longlining is considered to be more effective than standard longlining for bigeye tuna in certain locations (Suzuki et al., 1977; Suzuki and Kume, 1982).

Longline vessels are categorized as deck-loaded motherships (200-1,000+ gross tons), foreign-based (50-1,000 gross tons) and home-based (30-500 gross tons). Currently, very few vessels greater than 300 gross tons or mothership category are in operation. The larger home-based vessels of 150-500 gross tons are generally modern, have super-cold (-40° to -60°C) freezing capability and can remain at sea for up to 3-4 months between fueling stops. These vessels travel to various distant fishing areas, log many months (10-14 months) away from home ports and land their catch directly in Japan. Smaller vessels usually do not have such capability and are based close to the fishing areas. Some vessels rely exclusively on transshipping their catch to consigned markets.

The Markets

Markets for the annual world catch of

ABSTRACT—Species composition of tunas caught by the large Asian longline fleets has shifted over time. Much of the observed change appears to be market driven, combined with changing economic conditions, as opposed to being driven by resource availability. As part of the strategy for change, the oriental longliners developed the ability to target on certain species with a gear previously thought relatively nonselective with respect to target species. Use of longline catch statistics for resource assessment requires an understanding of the reasons for changes in the data to avoid misuse of the statistics.

The authors are with the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037.

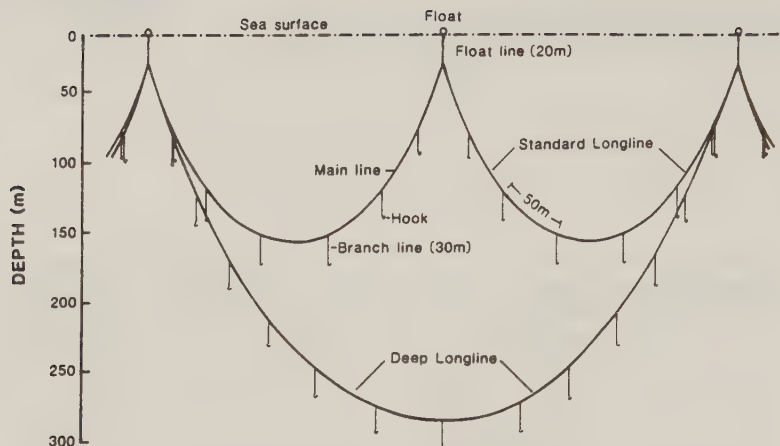


Figure 1.—Standard and deep longline gear as used by Japanese fishermen. The standard gear has an average of 6 branch lines per basket of mainline; deep-longline gear has about 13 branch lines (adapted from Suzuki et al., 1977).

about 400,000 metric tons (t) of longline caught tunas are primarily two: Canned tuna market and “sashimi” market. The canned tuna market has a less stringent fish quality requirement than the sashimi market. Most of the fish for the canned tuna market are caught, refrigerated, and transhipped frozen to cannery facilities. Since the United States is the largest consumer market for canned tuna, consuming in excess of 50 percent of the world’s canned tuna production (consumed about 730,000 t in 1984¹), a significant portion of the longline catch available for canning purposes is sold to U.S. canneries. Thus, U.S. tuna ex-vessel prices and import purchases have a significant effect on the world tuna market.

Data on annual U.S. imports of frozen tuna for the past 20 years (1965-85) show fluctuations in volume (Fig. 2). Much of the fluctuation is due to imports of skipjack tuna, which are not generally caught on longline gear. Imports of the larger tunas (albacore, *Thunnus alalunga*; yellowfin tuna, *T. albacares*; and bigeye tuna, *T. obesus*), which are caught by longliners, show little change in volume over the 20 years, averaging about 75,000 t of albacore and 50,000 t of com-

bined yellowfin and bigeye tuna per year. In other words, over the past 20 years there has not been any significant growth in the demand for longline-caught tunas in the world’s largest canned tuna market.

Albacore has traditionally commanded a higher price than yellowfin or bigeye tuna in the U.S. market and is packed exclusively as “white meat” tuna. Yellowfin and bigeye tunas along with skipjack tuna, *Euthynnus pelamis*, are used in “light meat” packs. Prices for these species move in tandem with each other because they are interchangeable in the pack.

In the United States, the ex-vessel prices of these “light meat” species showed an upward trend from 1965 to 1981 followed by a downward trend which has continued into 1986 (Fig. 3). The fall in price has been faster for albacore than for yellowfin and bigeye tunas.¹ In 1985, the U.S. prices returned to a level equal to those in 1977 and 1978.

Japan is virtually the sole market for sashimi, or tuna consumed raw. This market is sensitive to both supply and quality (particularly freshness, color, firmness, and fat content) and generally deals with large tunas. About 340,000-360,000 t of both fresh and super-cold frozen tuna are sold annually by the

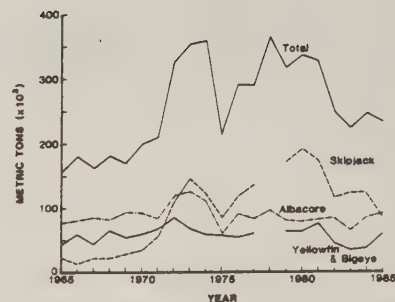


Figure 2.—Tonnage of fresh and frozen tuna by species imported into the United States. Source: Fisheries of the United States, various years.

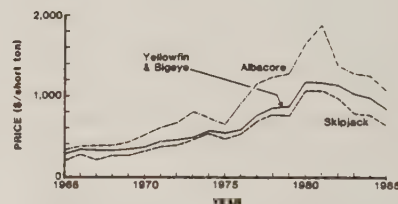


Figure 3.—Average ex-vessel prices paid for tuna delivered to U.S. canneries. Source: NMFS, Terminal Island, Calif.

sashimi market. This market has not shown significant growth since the 1960’s².

About 75 percent of the market is super-cold frozen tuna landed primarily by longliners. Japanese longliners supply most of the tuna, although recently Taiwanese and particularly Korean longliners have exported a significant amount of tuna to this market. Korean and Taiwanese vessels are supplying this market with about 90,000-120,000 t annually² and land most of their catch directly in Japanese ports (Uyemae, 1975).

Prices for sashimi-quality tuna in Japan are quite variable. In general, highest prices are paid for bluefin tuna, *T. thynnus* (southern and northern) followed by bigeye tuna, yellowfin tuna,

¹Herrick, S. F., Jr., and S. J. Koplin. 1985. U.S. tuna trade summary, 1984. Natl. Mar. Fish. Serv., SWR Admin. Rep. SWR-85-06, 24 p.

²Fujinami, N. 1986. Option for distant water countries. Manuscr. pres. at Tuna Workshop on Options for Cooperation in the Development and Management of Global Tuna Fisheries, 29 June-3 July 1986, Vancouver, B.C., 16 p.

Figure 4.—Average wholesale price of sashimi-grade tuna sold at the Yaizu fish market in Japan.
Source: Shingu et al., 1980.

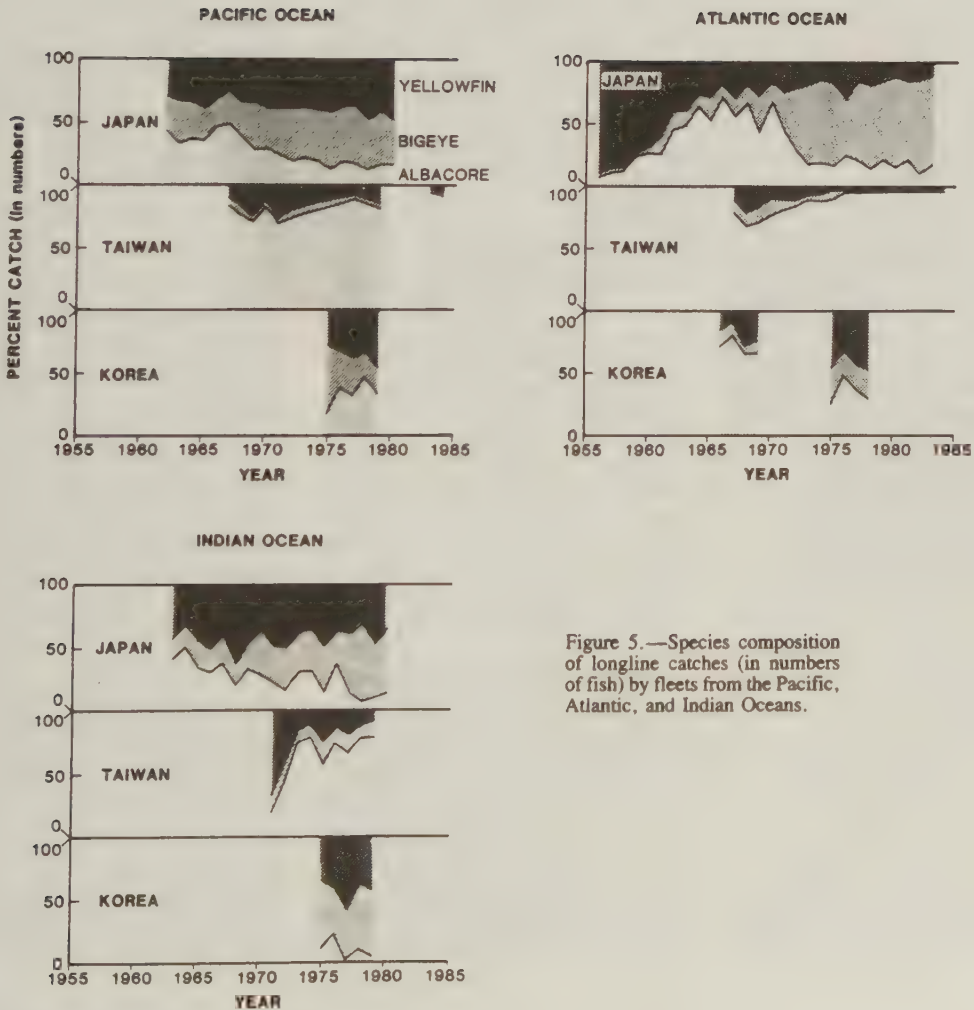
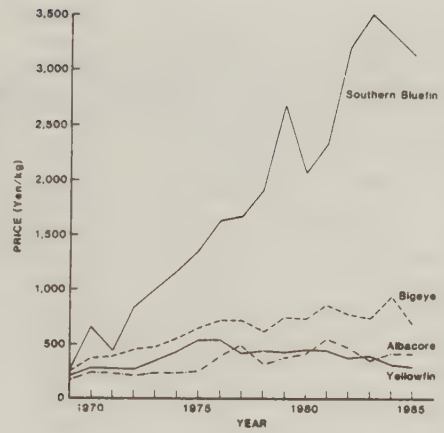


Figure 5.—Species composition of longline catches (in numbers of fish) by fleets from the Pacific, Atlantic, and Indian Oceans.

and albacore in that order (Fig. 4). To ensure the highest prices, longliners that fish tuna for this market must maintain high fish quality by landing the tuna fresh or by freezing the tuna with super-cold freezing equipment and landing them directly in Japan.

Global Patterns

Catches for the Japanese, Korean, and Taiwanese fleets were tabulated by ocean and species from published records: "ICCAT Statistical Bulletin" (ICCAT, Madrid), "Annual report of effort and catch statistics by area on Japanese longline fishery" (Fisheries Agency of Japan, Tokyo), "Annual report of catch and effort statistics and fishing grounds on Korean tuna longline fisheries" (Fisheries Research and Development Agency, Pusan), and "Annual catch statistics of Taiwanese tuna longline fishery" (Tuna Research Center, Taipei). A pattern can be seen in the proportion of species in the catch of the different fleets (Fig. 5). The data clearly show a fleet-specific pattern that is fairly independent of the ocean fished.

The Japanese fleet aggressively pursued yellowfin tuna and albacore until about 1970 to supply the growing U.S. canned tuna market. Then the fleet began a gradual and dramatic switch to bigeye tuna, which currently accounts for more than 50 percent of the catch. This switch to bigeye tuna is probably less a reflection of changes in the relative availability of the species, and more a reflection of changes in Japanese government policies and market forces, because the timing of the shift was the same in all oceans.

In the 1970's, fuel oil prices began to rise substantially, e.g., \$0.03/l in 1970 versus \$0.06/l in 1973², and fuel actually became unavailable in some strategically located ports used by the Japanese fleet (Uyemae, 1975). In 1970, high mercury levels in tuna were reported, and U.S. canneries refused to buy the large tunas because they often contained high levels of mercury (Peterson et al., 1973). Japanese labor costs also increased as the overall Japanese economy grew and prospered.² At the same time, the emergence of the 200-mile economic zones resulted in increased costs to vessel owners as license fees had to be paid for ac-

cess to some choice fishing areas. Ex-vessel prices of tuna for canning, on the other hand, were rising only about half as fast as costs (Fig. 3). This resulted in several bankruptcies and threatened the long-term survival of the entire Japanese fleet. The strategy adopted by Japan to cope with these economic forces was threefold: 1) a 21 percent reduction in the number of vessels between 1975 and 1984, while retaining the more efficient vessels²; 2) greater utilization of the super-cold freezing technology to produce quality fish for the sashimi market; and 3) the value of each load of tuna was enhanced through emphasis on higher valued species. In other words, the strategy was to reduce production that supplied the low-valued export canning market (100 percent in 1955) and to emphasize production of tunas to supply the high-valued sashimi market of Japan (80 percent in 1985).² Since bigeye tuna commands a higher price than yellowfin tuna or albacore in the sashimi market (Fig. 4), Japanese longliners began using special techniques to enhance their catch of bigeye tuna.

A discussion of events shaping this global pattern would not be complete without mention of events in the Japanese southern bluefin tuna fishery. The development of this fishery was spurred by high catch rates combined with a strong demand for southern bluefin tuna in the sashimi market and development of the super-freezing technology. Prior to the development of the super-cold freezing technology, longlined bluefin tuna destined for the sashimi markets from distant waters in the southern Indian and Pacific Oceans had to be quickly caught and transported to Japan at high cost. The super-freezing technology reversed this need for swift vessels and short fishing trips.

The strong market for southern bluefin tuna contributed to increasing fishing effort and catch and catch rates began to decline in the early 1960's. The stock began showing the effects of overfishing as the number of small fish in the catch increased and the catch rate declined with increasing effort (FAO, 1980; Murphy and Majkowski, 1981). In 1972, faced with substantial hikes in fuel prices and declining catch rates, the Japanese fleet

was in financial trouble. The fleet adopted voluntary measures to stabilize fishing effort in this fishery (ICCAT, 1986). Despite this, catch and catch rates continued to fall. We suspect that difficulties in this major Japanese longline fishery precipitated the adoption of a new strategy. The new strategy allowed the Japanese to shift excess capacity out of the southern bluefin tuna fishery into an underdeveloped bigeye tuna fishery to supply the domestic market, while retaining its modern, specialized longliners with super-cold freezing capacity.

Taiwan entered the longline industry during a period when the Japanese fleet was undergoing modernization and expansion in the late 1950's to early 1960's (Uyemae, 1975). Used Japanese vessels were purchased and put into operation by Taiwanese fishermen. They quickly specialized in production of the high-valued albacore for export to the U.S. canning market. Vessels were primarily based in foreign ports, close to the fishing areas and their catch either landed at a cannery port (e.g., American Samoa) or transhipped to canning facilities (e.g., Puerto Rico).

During the 1970's, when the Japanese fleet switched to catching bigeye tuna, the Taiwanese fleet benefited by the reduced competition. Apparently, unlike the Japanese fleet, lower operating costs, particularly for labor, and marginal increases in tuna prices allowed this fleet to continue to survive on catches of albacore for the canned tuna market during the 1970's. Recently, however, sharp declines in the price of albacore have caused cutbacks in operations of this fleet (Yang, 1985), but albacore production continues to be the strategy followed by most of the Taiwanese vessels. More than 80 percent of the catch currently is of albacore.

Like the Taiwanese fleet, used Japanese vessels were purchased by Koreans in the mid-1960's and put into operation from foreign bases to supply U.S. tuna canneries (Uyemae, 1975). Korean fishermen quickly discovered that this market was not growing for longline-caught fish. Rising fuel prices and marginal increases in tuna prices also threatened profitability. These realizations, along with encouragement from

Japanese trading companies, caused some vessels to switch fishing for the canned tuna market and to concentrate on the higher value sashimi market. The Koreans were successful in adapting technology for fishing bigeye tuna and in using import privileges that allowed direct landings in Japan. By 1974, direct landings by Korean longliners in Japan were 40,000 t of primarily sashimi-grade tuna (Uyemae, 1975). Further advances included adopting supercold freezing capability and acquiring larger vessels resulted in the current catch pattern for the Korean fleet being nearly identical to that of the Japanese fleet (Fig. 6). By 1982, Korean vessels landings in Japan grew to 56,000 t. The net effect for the Korean fleet is an evolution from solely supplying the canned tuna market to supplying primarily the sashimi market. This has placed this fleet in direct competition with the Japanese fleet and has caused disruption of the once orderly Japanese sashimi market as supplies from Korean vessels have contributed to surpluses substantially above the demand³. Continued access to the Japanese market will likely determine the economic survival of the Korean fleet.

Patterns in the Atlantic

Over the past decade, longliners accounted for the major share of the bigeye tuna catch from the Atlantic, more than 62 percent (Kume, 1985). In 1984 the total bigeye tuna catch of the Atlantic Ocean was 64,600 t, of which 64 percent was taken by longliners. Japanese longliners caught 24,300 t, Korean longliners caught 10,900 t, Taiwanese longliners caught 800 t and other nations the remainder.

The catch is principally taken in three regions (Fig. 7): A) northwestern Atlantic, off the U.S. and Canadian coasts; B) northeastern Atlantic from Cape Verde to Azores; and C) southeastern Atlantic off Angola and Namibia (Sakagawa, 1976). Longline fishery statistics for these three regions were tabulated by

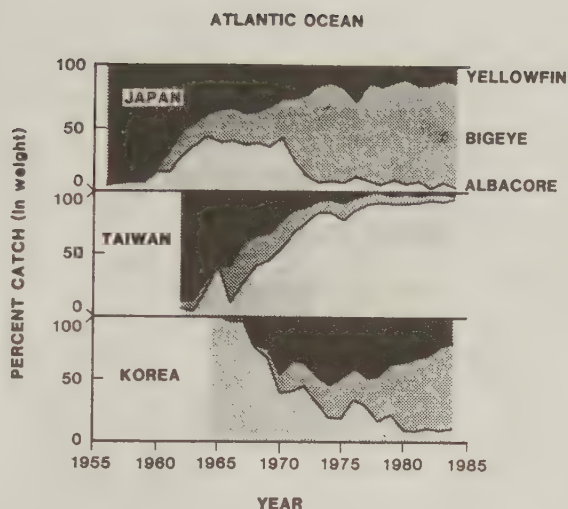


Figure 6.—Species composition of longline catches (in weight) from the Atlantic Ocean.

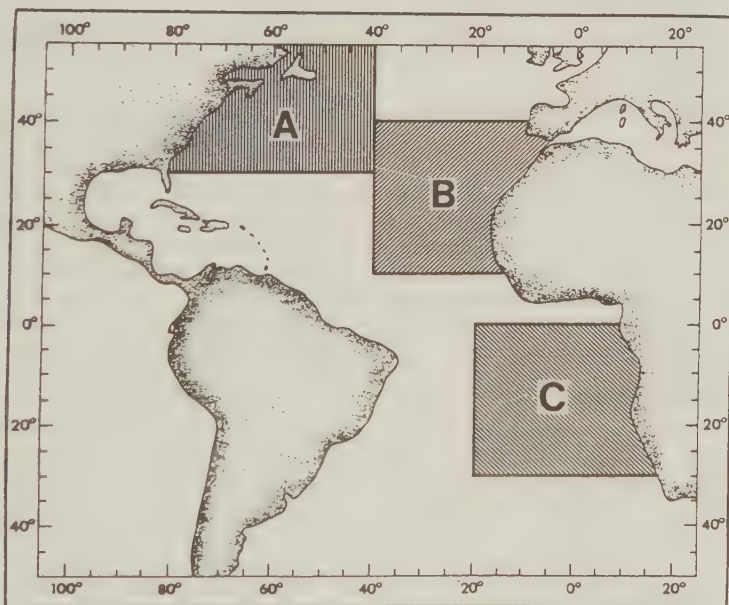


Figure 7.—Major longline fishing regions for bigeye tuna in the Atlantic Ocean.

³Yamashita, H. 1986. Current trends in industry, Japan. Manuscr. pres. at Tuna Workshop on Options for Cooperation in the Development and Management of Global Tuna Fisheries, 29 June-3 July 1986, Vancouver, B.C., 16 p.

fleets. The purpose was to determine whether the ocean-wide profile would persist if the data were tabulated on a

smaller, regional scale and whether the patterns are related to variation in fishing effort.

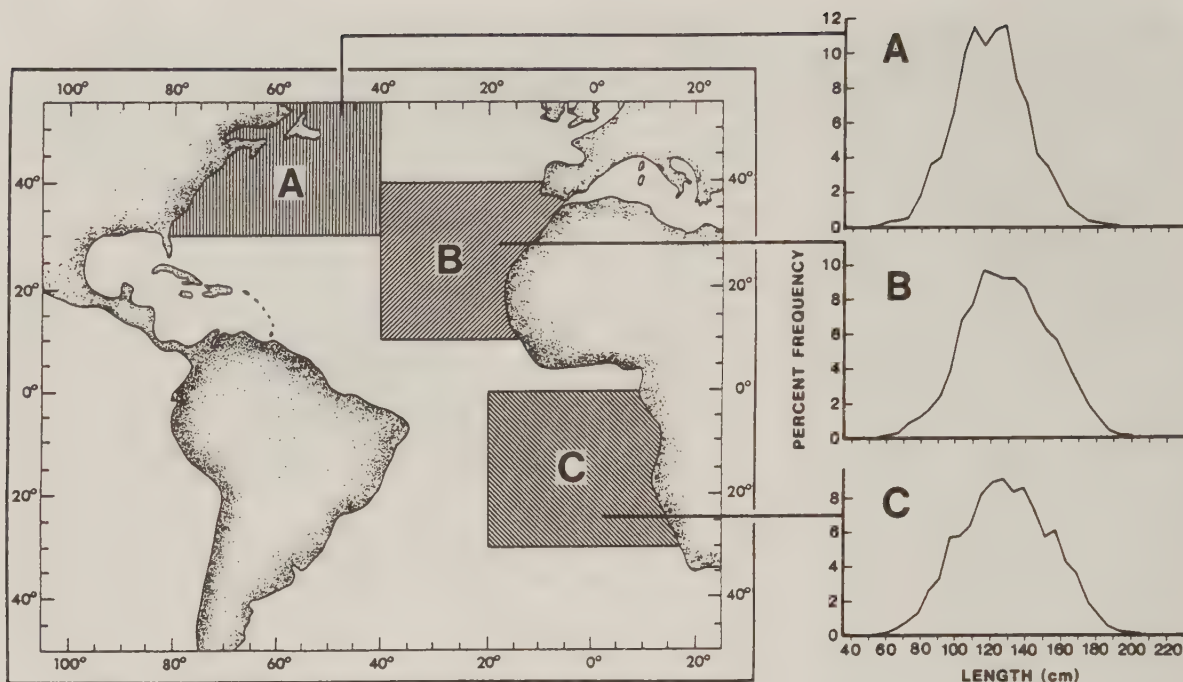


Figure 8.—Size composition of bigeye tuna caught by longliners in the bigeye tuna fishing regions of the Atlantic.

The sizes of bigeye tuna caught in the three regions are identical and consist of fish that are primarily of spawning age (Fig. 8). This consistency in size frequency has led to the general belief that the longline gear is selective in catching only large sizes of bigeye tuna.

Species Composition

The species composition profiles based on numbers of fish or weight show particular patterns. For the Japanese fleet, regions B and C yield primarily bigeye tuna, but region A yields about an equal mixture of both bigeye tuna and albacore (Fig. 9).

The Taiwanese fleet has a profile that is consistent for all three regions when viewed by numbers or weight, i.e., predominantly albacore (Fig. 9). In regions B and C, which Japanese data indicate are bigeye tuna fishing areas, less than 10 percent of the Taiwanese catch is bigeye tuna and more than 80 percent is albacore. In terms of numbers, Taiwanese

longliners caught 191,000 albacore in region B and 203,000 albacore in region C in 1983. Japanese longliners caught only 5,000 albacore in region B and 4,000 albacore in region C, but bigeye tuna catches were high, 69,000 and 188,000, respectively, in 1983.

Time series of Korean longline statistics are incomplete, but, from data available for comparison, this fleet seems to be the most flexible and adaptive of the three fleets (Fig. 9). In region A, albacore is the target species; in region B, both yellowfin and bigeye tuna are targets; in region C it is bigeye tuna.

The conclusion is that the ocean-wide patterns persist in the three regions for the Taiwanese fleet, two regions for the Japanese fleet, and one region for the Korean fleet. Thus, regional fishing areas and fleet operations both determine what species are caught and their ratio in the catch.

Catch Rates

It might be argued that patterns in species composition of the catch are due to a normal evolution of a multispecies fishery in which declining catch rate for one species results in switching to another species with a higher catch rate. We examined this hypothesis using nominal catch rates by fleets and regions.

The catch rates for the Japanese fleet vary within a region, but there is a clear pattern (Fig. 10). The high catch rates for albacore (average of 30 fish/1,000 hooks in regions A and C) were followed by sharp declines in the early 1970's when switching to bigeye tuna occurred. This was followed by a leveling off of the albacore catch rate at a low level. The catch rate for bigeye tuna in comparison shows less variation. Since 1970 it has fluctuated between 5 fish/1,000 hooks and 20 fish/1,000 hooks, and since 1974 it has surpassed the albacore rate in nearly all years. The effect of deep longlining, i.e.,

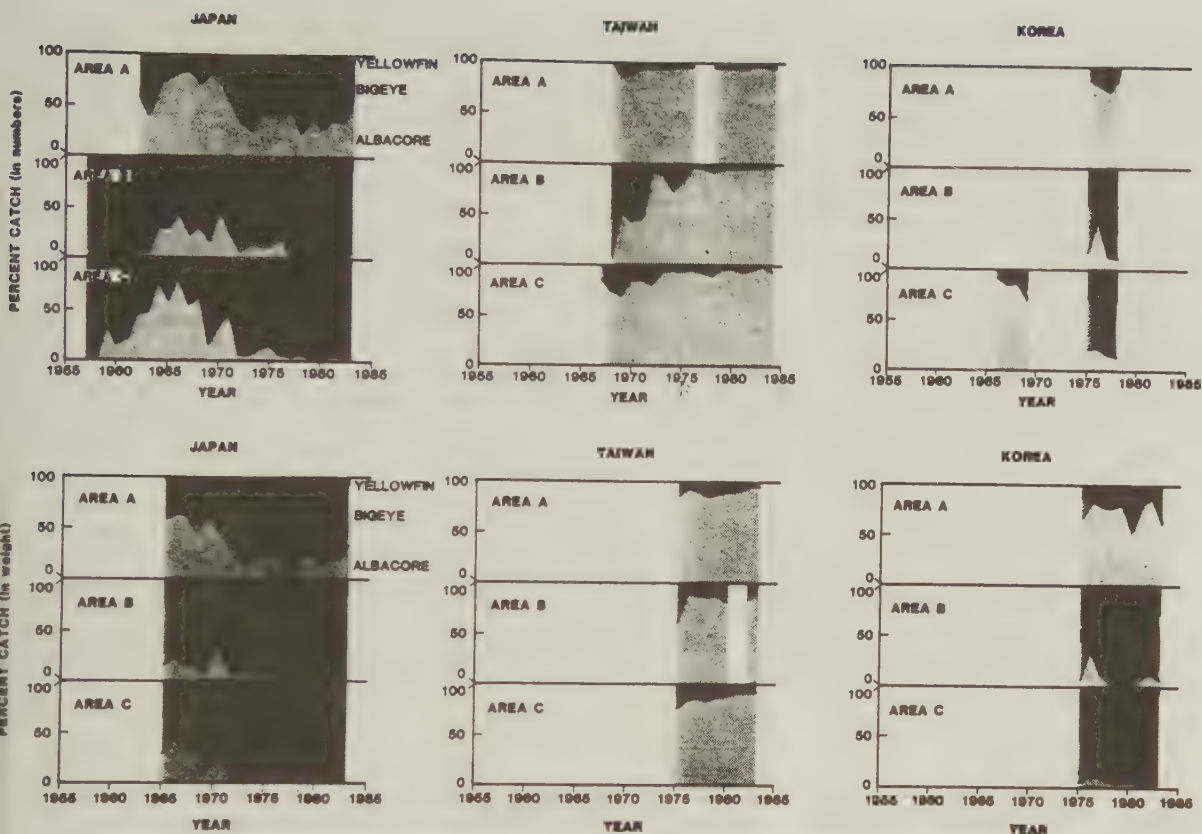


Figure 9.—Species composition of longline catches (in numbers of fish and weight) by fleets from bigeye tuna fishing regions of the Atlantic Ocean.

superior catch rate for bigeye tuna, since 1978 is not evident in the data possibly due to limited amounts of effort by this gear; so, we conclude that its effect, if any, is negligible.

In comparison, the Taiwanese fleet shows catch rates of albacore that are high although variable (Fig. 10). The catch rates are comparable to rates that the Japanese fleet was experiencing before the switch to bigeye tuna occurred in the early 1970's and are substantially higher than catch rates for bigeye tuna. The reduced competition by Japanese longliners for albacore in region B appears to have contributed to improved catch rates for Taiwan longliners operating in that region. The Taiwanese fleet appears to have selected the species with the highest catch rate.

Incomplete data for the Korean fleet prevent a thorough analysis. However, available data (Fig. 10) suggest that the pattern of catch rates is more like that of the Japanese fleet than the Taiwanese fleet.

These results indicate that the hypothesis that declining catch rate of one species triggers switching to another species with a higher catch rate in longline fisheries is unsupported. Nominal catch rates for albacore in all three regions are substantially higher than for bigeye tuna or yellowfin tuna, yet only the Taiwanese fleet concentrates on fishing for albacore. The Japanese fleet abandoned the high catch rates for albacore in 1970-71 to concentrate on bigeye tuna with a lower catch rate. Similarly, the Korean fleet is not pursuing the species with the highest

catch rate, but concentrating on a mixture of species dominated by bigeye and yellowfin tunas.

Fishing Effort

Another factor that might explain the difference in patterns in species composition is the seasonal distribution of fishing effort. Seasonal variation in longline fishing effort within regions of the Atlantic Ocean is well known (Shingu et al., 1980; Yang, 1980). But is the variation so different between the Japanese and Taiwanese fleets to cause one fleet to catch a significantly higher proportion of bigeye tuna while the other does not?

The seasonal pattern of fishing effort by fleet for 1983 (Fig. 11) indicates that in region A, both fleets have similar patterns. In region B, the Japanese fleet em-

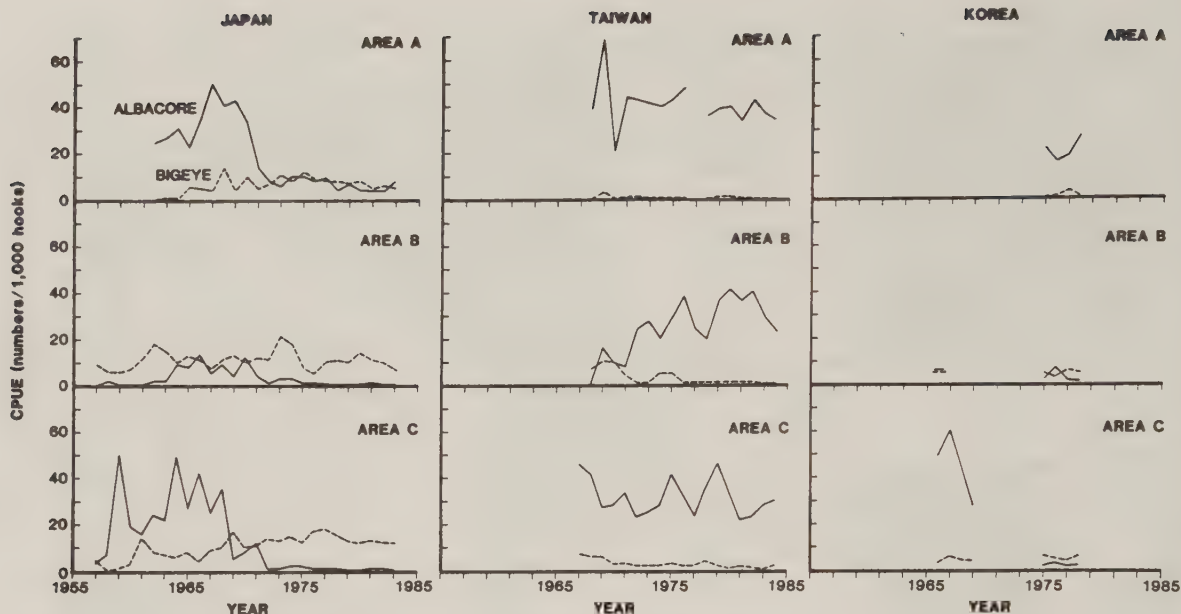


Figure 10.—Catch rates for longline fleets fishing in the bigeye tuna fishing regions of the Atlantic Ocean.

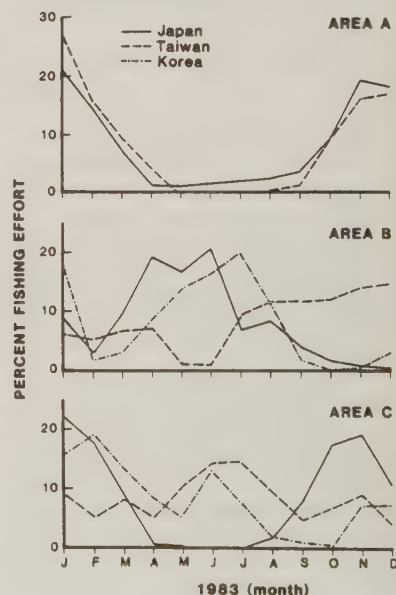
phasizes spring and summer months, whereas the Taiwanese fleet emphasizes the summer and fall. In region C, the difference is in the spring and summer months when the Japanese fleet is not operating, whereas the Taiwanese fleet is active.

Within regions B and C, besides differences in seasons fished, fishing effort for the Japanese fleet tends to be concentrated towards the equator, whereas the Taiwanese fleet concentrates in areas toward the poles. Thus, in regions B and C, seasonal differences in fishing effort are a factor causing more of one species to be caught than another. However, this is obviously not the sole factor, since in region A the two fleets fishing similar locations and seasons but caught different proportions of tuna species.

Basis for Patterns

Longlining is considered a labor-intensive form of fishing with catch rates relatively low compared with other forms of tuna fishing. Fuel and labor constitute 75 percent of the expenses of operating a longline vessel (Uyemae, 1975). It is estimated that a 300 gross ton Japanese ves-

Figure 11.—Seasonal distribution of fishing effort for the Japanese and Taiwanese longline fleets by bigeye tuna fishing regions of the Atlantic Ocean.



sel spends about \$500,000 for expenses on a 10-month fishing trip which, on the average, results in a full load (Uyemae, 1975). Obviously, even at the highest historical prices offered by U.S. canneries (Fig. 3), a longliner can barely break even, whereas with prices for sashimi-grade bigeye tuna (about \$2,300/t) a profit is possible. Market forces thus have played a major role in influencing the fleets to specialize and concentrate on certain species.

These market forces through time have influenced the operations of the longline fleets and have shaped their strategy so

that each specializes in certain species for particular markets. This is remarkable, given that the longline gear is often

thought of as an indiscriminate, nonselective gear. It is obvious that in skillful hands, this gear is capable of being deployed to catch a particular mix of tuna species with significantly different proportions of one species over another. How this is done has not yet been fully explained.

Hanamoto (1976) contends that the deeper the branch lines are the greater the catch of bigeye tuna. Suda et al. (1969) postulated that the habitat of bigeye tuna is between the mixed layer and subpolar waters, i.e., in the thermocline region. Depending on how the gear is deployed relative to the thermocline and the preferred temperature of 20°C bigeye tuna would be caught. Suzuki and Kume (1982) conducted an experiment to test this hypothesis in the western Pacific Ocean. Their experiment yielded highest bigeye hook rates for the deepest sets (up to 225 m) and good catches in and below the thermocline in temperatures of 11°-26°C. Their good catches, however, were for both yellowfin and bigeye tunas in approximately the same proportions.

A series of similar experiments were carried out by Laurs and coworkers⁴ (Laurs et al., 1981) in exploratory fishing for albacore in the eastern north Pacific Ocean. They used vertical and horizontal temperature profiles to select fishing areas and to position their longline gear. They concluded that thermal fronts with temperatures of 16°-19°C tend to concentrate albacore. Good catches of albacore were obtained while fishing in the top half of the thermocline where the 16°C isotherm was located. Their experiment produced catches of both albacore and bigeye tuna, but albacore made up more than 90 percent of the catch.

Tracking experiments of tunas tagged with ultrasonic transmitters have been conducted to study the vertical and horizontal movements of tunas. While experiments so far have used tunas smaller than those of average size in longline catches, which may make the results somewhat atypical for larger fish, the re-

sults do provide biological support for the hypothesis that albacore, bigeye, and yellowfin tunas are relatively separated in the water column. Results of sonic tracking of albacore^{4,5} show that albacore tend to occupy the upper portion of the thermocline during daylight hours with few radical excursions above or below the thermocline. At night albacore are found above the thermocline with rather large excursions upward and downward below the thermocline. By contrast, bigeye tuna were found generally below the thermocline, deeper at night than during the day.⁶ Yellowfin tuna tend to swim deeper than albacore but not as deep as bigeye tuna and prefer the warmer mixed layer.

A definitive explanation of how the fleets specialize in catching particular tuna species is not possible without more detailed observations on the actual operations of the vessels and on the behavior of large tunas typically caught by the fleets. However, some understanding of "how" is emerging from findings so far.

A combination of several factors appears to be used by the fleets in catching selective species. Season is one, but perhaps most important are areas fished and gear deployment. Fishing for albacore is concentrated in temperate regions where albacore is the dominant species and where they occur frequently along thermal fronts created by polar waters meeting warmer waters. The 16°C isotherm is used as an indicator of preferred water. Vertically, fishing in the thermocline or just above it in 16°-19°C waters assures catches to be predominantly albacore.

Fishing in the tropical and subtropical regions results in primarily bigeye and yellowfin tuna catches. Yellowfin tuna occupies primarily the mixed layer but extends into the thermocline. Bigeye tunas are found deeper, within the thermocline and below in 11°-26°C water. Gear deployment in these regions requires more skill for targeting on one spe-

cies. The gear is probably fished in the lower half of the thermocline and slightly below for enhanced catches of bigeye tuna. Electronic equipment, probably chromoscopes, are used to find bigeye tuna more accurately in and below the thermocline and for precise deployment of the gear.⁷

The results of our review point out the role of market forces in determining the species composition of the longline catch and of technological developments in providing fishermen with the capability to effectively target on certain species. Our results also point to the need for extreme caution in utilizing a time series of longline fishery statistics to determine stock condition without a thorough understanding of the underlying economic events that influenced the time series of data. The frequent assumption made when using such statistics is that the catchability of a unit of longline fishing effort remains constant throughout a time series. This assumption is obviously not true. The fleets have evolved in response to forces that are not completely biological. The data on catch and catch rates must be adjusted to account for these responses, and it is likely that current practices do not fully accomplish this.

Acknowledgments

Our study benefited from advice and information of colleagues who have many years of experience with tuna fisheries. We wish to acknowledge the assistance of S. Koplin and S. Sonu of the Southwest Region, National Marine Fisheries Service for compiling difficult-to-obtain statistics; S. Herrick of the Southwest Fisheries Center (SWFC) for information on global tuna trade; and R. Dotson of the SWFC for information on design and deployment of longline gear for tunas. We thank many other colleagues for their careful review of this manuscript and for providing constructive comments.

Literature Cited

- FAO. 1980. State of selected stocks of tuna and billfish in the Pacific and Indian Oceans. Food
- ⁴Laurs, R. M., R. Lynn, R. Dotson, R. Nishimoto, K. Bliss, and D. Holts. 1982. Exploratory albacore longline fishing in the eastern north Pacific during winter 1982. Natl. Mar. Fish. Serv., SWFC Admin. Rep. LJ-82-06, 79 p.
- ⁵Bartoo, N. W., and S. Kume. 1982. Report of the Sixth North Pacific Albacore Workshop. Natl. Mar. Fish. Serv., SWFC Admin. Rep. LJ-82-02, 24 p.
- ⁶Holland, K., and R. Brill. 1984. Progress on ultrasonic tracking of FAD-associated yellowfin tuna. In A. E. Dizon (editor), Proceedings of the 35th Annual Tuna Conference, p. I. Natl. Mar. Fish. Serv., SWFC Admin. Rep. LJ-84-35.
- ⁷Dotson, R. NMFS Southwest Fisheries Center, La Jolla, Calif. Personal Commun.

- Agric. Organ. U.N. Fish. Tech. Pap. 200, 88 p.
- Hanamoto, E. 1976. The swimming layer of bigeye tuna. *Bull. Jpn. Soc. Fish. Oceanogr.* 29:41-44. Southwest Fish. Cent., Honolulu Lab., transl from Jpn.
- ICCAT, 1986. Report for biennial period, 1984-85 (Part 2 1985) (Engl. version). *Int. Com-miss. Conserv. Atl. Tunas*, Madrid, 291 p.
- Kume, S. 1985. An analysis on the stock abundance of Atlantic bigeye tuna caught by Japanese longline fishery. *ICCAT, Collect. Vol. Sci. Pap.* 23(2):248-253.
- Laurs, R. M., R. J. Lynn, R. Nishimoto., and R. Dotson. 1981. Albacore trolling and long-line exploration in eastern north Pacific waters during mid-winter 1981. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-SWFC-10, 40 p.
- Lee, J. U. 1986. Aspects of fishing effort of Korean tuna longline fishery exerted to the Atlantic yellowfin and bigeye tuna. *ICCAT, Collect. Vol. Sci. Pap.* 25:99-103.
- Murphy, G. I., and J. Majkowski. 1981. State of the southern bluefin tuna population: Fully exploited. *Aust. Fish.* 40(11):20-29.
- Peterson, C. L., W. L. Klawe, and G. D. Sharp. 1973. Mercury in tunas: A review. *Fish. Bull.* (U.S.) 73:603-614.
- Sakagawa, G. T. 1976. Status of the bigeye tuna stocks of the Atlantic Ocean, 1957-73 from production model analysis. *ICCAT, Collect. Vol. Sci. Pap.* 5(1):176-184.
- Shapiro, S. 1948. The Japanese tuna fisheries. U.S. Dep. Int., Fish Wildl. Serv., Fish. Leaflet. 297, 60 p.
- Shingu, C., K. Hisada, and Z. Suzuki. 1980. Description of the Japanese longline fishery for bluefin tuna in the Atlantic. *ICCAT, Collect. Vol. Sci. Pap.* 11:145-160.
- Suda, A. 1974. Recent status of resources of tuna exploited by longline fishery in the Indian Ocean. *Bull. Far Seas Fish. Res. Lab.* 10:27-62.
- _____, S. Kume, and T. Shiohama. 1969. An indicative note on a role of permanent thermocline as a factor controlling the longline fishing ground for bigeye tuna (Engl. summ.). *Bull. Far Seas Fish. Res. Lab.* 1:99-114.
- Suzuki, Z., Y. Warashima, and M. Kishida. 1977. The comparison of catches by regular and deep tuna longline gear in the western and central equatorial Pacific. *Bull. Far Seas Fish. Res. Lab.* 15:51-89.
- _____, and S. Kume. 1982. Fishing efficiency of deep longline for bigeye tuna in the Atlantic as inferred from the operations in the Pacific and Indian Oceans. *ICCAT, Collect. Vol. Sci. Pap.* 17(2):471-486.
- Ueyanagi, S. 1974. A review of the world commercial fisheries for billfishes. p. 1-11. *In* R. Shomura and F. Williams, (editors), *Proceedings of the International Billfish Symposium*, Kailua-Kona, Hawaii, 9-12 August 1972, Part 2. Review and contributed papers, p. 1-11. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.
- Uyemae, J. 1975. The economy of the tuna fishery in Japan. Bungei Shinji, August, p. 340-350. Southwest Fish. Cent., Honolulu Lab., transl. from Jpn.
- Wise, J. P., and P. W. Miyake. 1982. General review of Atlantic tuna fisheries, *In* 2 Semana das Pescas dos Acores, Secretaria Regional da Agricultura e Pescas, Acores, p. 73-102.
- Yang, R. T. 1980. Distribution of fishing effort and catch of albacore by Taiwan's tuna longline fleet in the north and south Atlantic Ocean, 1972-78. *ICCAT, Collect. Vol. Sci. Pap.* 91(2):326-337.
- _____. 1985. National report of Taiwan. *In* Report for biennial period, 1984-85 (Part 1 1984), p. 289-290. (Engl. version). *Int. Com-miss. Conserv. Atl. Tunas*, Madrid.

TUNA TAGGING IN THE PHILIPPINES, THAILAND, AND MALAYSIAN WATERS

Richard S. Shomura
Southwest Fisheries Center Honolulu Laboratory
National Marine Fisheries Service, NOAA
2570 Dole Street
Honolulu, Hawaii 96822-2396

INTRODUCTION

During the past decade, world tuna landings increased markedly; especially active have been the fisheries in the western Pacific Ocean. In 1985, the total world tuna and billfish landings were reported in FAO statistics (FAO 1985) as 3.15 million metric tons (mt), an increase of 63% over landings for 1975. Landings in the Pacific Ocean for 1985 were 2.05 million mt, representing 65% of the world landings. The importance of the western Pacific Ocean is exemplified by the FAO statistical area 71 (Figure 1), in which 29 of the 48 world-recognized scombrid species occur (Collette and Nauen 1983) and catch represents 49% of the Pacific landings for 1985 (FAO 1985).

In an effort to understand more about the tuna resources in the western Pacific Ocean, the Indo-Pacific Tuna Development and Management Programme (IPTP) in 1983-84 cooperatively undertook a tuna tagging study with the Government of Indonesia. The study's results are summarized in Phuket tuna meeting report (FAO 1986). To broaden the tagging program, the IPTP engaged the author of the present report to formulate a plan to conduct tuna tagging in Philippines and Thailand-Malaysian waters.

The terms of reference of this consultancy were as follows:

- (1) detail major objectives of tuna tagging in the region,
- (2) list target species and number of fish expected to be tagged,
- (3) describe the fishing vessel and gear to be used,
- (4) develop a time schedule,
- (5) calculate budget estimates, and
- (6) detail the arrangements to implement the project.

Prior to preparing this report, the author visited the Philippines (Manila and General Santos City), Thailand (Bangkok), and Malaysia (Penang) to consult with fishery officials, tuna scientists, and industry representatives (Appendix Table A). The tour was to include Indonesia; however, time constraints prevented this portion of the consultation to be completed.

REVIEW OF TUNA TAGGING

In developing the strategies for tuna tagging in the Philippines and the Thailand-Malaysia regions, considerable value was gained in reviewing previous tuna tagging efforts. The following sections briefly summarize the results of this review.

Tags

The Atlantic bluefin tuna (*Thunnus thynnus*) was the first tuna species for which movement was described by tagging information. In 1961, a bluefin tuna landed off Bergen, Norway (Mather 1962) was determined to have originated in the Mediterranean Sea, based on the type of hook found embedded in the tuna's mouth. Although the tagging was inadvertent, the results demonstrated the value of tag placement on pelagic fishes.

Not until the 1950's was a concerted effort made by directed tagging programs to describe the movement of tunas in the eastern Pacific. The California Division of Fish and Game began using plastic loop tags on tunas in 1953 (Wilson 1953). The tag information (tag number and where the tag should be returned) was written directly on the plastic tubing. The tubing was inserted through the upper portion of the fish (posterior of the second dorsal fin) with the aid of a stainless steel tubing. The tag was secured by tying both ends together.

The loop tag was not very satisfactory because it was time consuming to affix the tag and, especially, to secure the ends. Although the latter was resolved by using a "figure eight" knot, tagging time remained a problem until the subsequent development of the dart tag. The dart tag consisted of a length of plastic tubing onto which a solid head with a single barb was affixed at one end. The standard procedure adapted was to secure the tag near the base of the second dorsal fin with the aid of a short length of stainless steel tubing. The tubing was sharpened at one end to permit ease in penetrating the tuna's skin.

The dart tag as described above has been used by research agencies in tagging various species of tunas, including the yellowfin (*T. albacares*), skipjack (*Katsuwonus pelamis*), bigeye (*T. obesus*), albacore (*T. alalunga*), northern bluefin (*T. thynnus*), and southern bluefin (*T. maccoyi*). Additional details of tuna and billfish tagging are reported by Bayliff and Holland (1986). The most extensive use of the dart tag to date has been the skipjack tagging program conducted by the South Pacific Commission (Kearney 1982).

Presently, there are several commercial manufacturers of dart tags: Floy Tag Co. (U.S.A.), Fuyo Sangyo Co. (Japan), and Hallprint, Pty, Co. (Australia). Based on limited interviews with scientists involved in recent tuna tagging experiments, the tags produced by Hallprint are highly recommended. Instead of dart heads that are secured to the tubing by glue, the Hallprint tag heads are molded onto the polyethylene tubing. An additional feature is that the tag consists of two pieces of tubing: An outer tubing protects the writing placed on the inner tubing from abrasion.

Method of Fish Capture for Tagging

Although tuna are taken by a wide range of fishing gear, the suitability of tuna for tagging purposes is limited to a few. The attributes of a good method of capture for tagging purposes include 1) the ability to release tuna in an "undamaged" and unstressed condition, 2) accessibility to a large number of fish, and 3) accessibility to the desired size of fish.

Table 1 provides a rough indication of the suitability of tuna for tagging, based on method of capture. The evaluation is generalized and subjective because some gear types are excellent for some tuna species but not for others; e.g., based on tag recoveries of 5-6% trolling apparently is a satisfactory method of capture for albacore tagging (Lauris and Wetherall 1981). Although not fully tested, it is unlikely that skipjack tuna caught by troll gear can be considered good candidates for tagging because their jaws are easily damaged by the gear. Furthermore, shore-side experiments conducted in Hawaii demonstrated that of the three tuna species (yellowfin, kawakawa, and skipjack) routinely maintained in captivity, skipjack tuna are by far the most susceptible to stress from handling, thus, leading to mortality (Queen and Brill 1983).

Of the several methods of capture evaluated for tuna tagging, the pole-and-line gear has been the most successfully used to date. Large numbers of small to medium sized tunas can be tagged over a short period, and time from capture to release is generally less than 10 seconds. Marr 1963 reported that skipjack tuna were tagged in less than 4 seconds in one tagging experiment; however, the fish were not measured.

The success of fish caught by purse seine for tagging has not been rated high; the problem probably rests with the long period it takes from the time the gear is set until tagging takes place. The tuna probably becomes highly stressed as the "pocket" becomes small enough for the taggers to retrieve the fish. The stress apparently causes physiological changes in the animal that result in delayed mortality. After extensive trials, the Inter-American Tropical Tuna Commission (IATTC) abandoned tagging of tunas caught by purse seine; the recovery rate of yellowfin tuna was judged to be lower than achieved by pole-and-line tagged fish. Also, of 1,363 skipjack tuna caught by purse seine and tagged only 15 (1.1%) were recovered (Bayliff 1973). If fish can be tagged from the early phases of the purse seine operation, the method could result in large numbers of good quality fish being tagged.

With the exception of gill nets, other methods of capture (troll, longline, and handline) can be used for tagging tunas; however, a major shortcoming of these methods is that substantially fewer fish are caught than by the pole-and-line or the purse seine methods. Also, there are some fish size limitations with these gears. The fish caught by gill net generally are landed dead or too badly damaged for tagging.

Recovery Rates

The time between capture and release of the tagged fish is crucial for successful recovery. Data verifying this factor are not abundant; however, it should be noted that the recovery rate in Hawaii of skipjack tuna tagged by loop tags was considerably lower than that of skipjack tuna tagged by dart tags (0.6 vs 9.28%); the dart tag can be applied substantially faster than the loop tag (Marr 1963).

Recovery rates of tagged fish should not be used as the sole criterion to measure success of a tagging project. Low recovery rates may simply reflect a large population base or that the fish migrated from the area and were not available to subsequent fishing effort. Nonbiological factors possibly contributing to low recovery rates include high tagging mortality, tag loss, and the nonreturn of tags after capture.

Table 2 provides some tag release and recovery data from previous tagging experiments. As noted above, the tag recovery rates should be viewed with caution.

Tag Rewards

Rewards have been used as a means to encourage the return of tags along with the necessary recovery data. These rewards range from gifts of printed T-shirts and caps to monetary gifts. Table 3 provides some examples of the types of rewards issued by previous tuna tagging programs. To emphasize the need for return of tags, most tagging programs have incorporated a system of annual lotteries, whereby monetary gifts are given to the selection of tag numbers representing tag returns from the previous year.

TUNA TAGGING IN THE PHILIPPINES

The tuna fisheries in the Philippines have shown a remarkable growth since 1971, when the total tuna catch for the Philippines was reported at 9.0 thousand metric tons. By 1985, the catch had risen to 261.6 thousand metric tons, and tuna landings represented 20% of the marine fish production of the Philippines. The principal fishing grounds are the waters off Mindanao Island; about 58% of the total tuna catch for the Philippines comes from this region although tuna are taken throughout the Philippine Archipelago. All tuna species are taken throughout the year; however, there appears to be a peak in August-September for the southern waters of Mindanao Island.

Of the 48 scombroid species recognized by tuna systematists (Collette and Nauen 1983) 29 species are in FAO statistical area 71, which encompasses the Philippines. The major part of the Philippines tuna catch, however, consists of five species: frigate and bullet tunas (36.6%), yellowfin tuna (24.6%), skipjack tuna (23.0%), and kawakawa (16.0%).

The types of gear used to capture tuna vary and include the purse seine (49%), ring net (35%), and bag net (13%). The remaining catch is made by drift gill nets, lift nets, seine nets, longline, handline, and troll gear. It should be noted that several of the gear types use the payaos as part of their fishing operations; e.g., ring-net gear and handline fishing by bancas.

Objectives of Tuna Tagging Program

Development of the tuna fisheries as a major industry in the marine production sector of the Philippine economy has given rise to a number of pertinent questions by the fishing industry and government agencies: 1) Can this catch be sustained? 2) What is the size of the resource base of the several tuna species being harvested? 3) What is the impact on the resource base of the large catches of small sized tunas associated with payaos? 4) Are the small sized tunas present around the payaos products of spawning in Philippine waters? 5) Not all size classes of tunas are present in the fishing grounds; what are their migratory pathways into and out of the region? 6) What are the interactions between gear? Although solutions to some these questions require information beyond that provided by tagging (e.g., detailed catch and effort data for stock assessment studies), a well-designed tagging program can provide a wealth of information regarding the dynamics of the tuna resources and the fisheries.

The objective of the present effort is to develop a tuna tagging technique that can form the basis for later tagging studies designed to address specific questions.

Method of Tagging

At the tuna meeting held in Phuket, Thailand, in August 1986, a recommendation was made to undertake tuna tagging in the southern Mindanao Island region (FAO 1986). A review of the fisheries based in General Santos revealed that ring-netting, handlining from bancas, and longlining were the principal methods used in the region. Reportedly, several bancas used a pole-and-line fishing operation with live bait to catch tunas in the region; this has not been confirmed to date.

Two of these three methods--handlining from bancas and longlining--were eliminated as potential sources for capturing tunas for the tagging project, because of the expected small catch and relatively large size of tunas. There are, however, several viable options as sources of tunas for tagging:

- (1) If a pole-and-line banca fishery exists, charter one bancas and conduct tagging via surface schools or by fishing around payaos; the latter would require prior arrangements with the payao owner.

- (2) Tag tuna caught by the ring-net fishery; tagging should take place after the "pocket" is small enough to catch fish for tagging.
- (3) Tag tuna caught by the ring-net fishery; modify tagging operations to reduce stress of tagged fish; several modifications could be included:
 - (a) operate in conjunction with pole-and-line fishing banca using live bait,
 - (b) pole-and-line fishing with lures only from a skiff immediately after the ring net has been set, and
 - (c) divert part of the commercial catch into a small net impoundment placed adjacent to the ring net; tagging can be done after commercial fishing has been completed.
- (4) Convert existing fishing vessel (e.g., trawler) to conduct pole-and-line fishing operations.
- (5) Charter a pole-and-line vessel from outside the region; e.g., a commercial pole-and-line vessel from Indonesia fishery.

Evaluation of Methods of Capture

The following provides some comments regarding each of the options listed above:

Option 1 is advantageous because the viability of fish caught for tagging by a pole-and-line operation is good. The disadvantages include the possible difficulty in obtaining adequate supplies of baitfish and the expected difficulty of tagging from a banca; e.g., limited space and the presence of two outriggers.

Option 2 would provide a very large supply of tuna, but the bulk of the catch probably would not be suitable for tagging. The latter could be tested by retaining tagged fish for 4-5 days in a small holding pen adjacent to the payao.

Option 3 also would provide a very large supply of tuna. The modifications (Options 3a-c), if successful, should lead to accessibility of good quality fish.

Option 4 has the advantage of a pole-and-line operation; thus, it has the potential of tagging large numbers of viable tuna. The disadvantages include the apparent lack of a steady supply of baitfish and the relative high cost of converting and operating a pole-and-line vessel over a short tagging period. During the South China Sea Programme, the Bureau of Fisheries vessel, Paeneus Monodon was converted into a pole-and-line vessel

at a reported cost of about \$(US)20-25 thousand (Lee 1978). Operational costs could conceivably amount to \$(US)20 thousand per month.

Option 5 has the same advantage as Option 4. The disadvantages include the possible lack of a steady baitfish supply and charter costs could equal about \$(US)25 thousand per month.

Projection of Fish to be Tagged

A mission report (FAO 1986) proposed a tagging goal of 20,000 tunas over a 1- to 2-month tagging program in the Philippines. At this time, projecting a meaningful number of fish to be tagged would be difficult because a proven tagging protocol has not been developed for this region. Furthermore, it is unlikely that the conventional pole-and-line method of tagging fish will be the eventual mode of operation for the Philippines; thus, experiences from other areas that use this tagging technique are not applicable to tagged fish projections in the Philippines. It should be noted that the IATTC and the SPC, two research organizations with extensive experience in tuna tagging, averaged about 250 fish tagged per fishing day. Individual highs exceeded 1,000 tagged fish by the SPC (Kearney 1970).

Rather than focus on a specific number of fish to be tagged, the present project proposed for the Philippines should be directed toward the development of a tagging protocol that could serve future tagging efforts in the region. Future tagging objectives will dictate the number of fish to be tagged and the time and space distribution of tagged fish.

Budget and Projected Time Schedules

Table 4 provides rough budget estimates for the several options noted in this section. Figure 2 gives some indication of the time schedules for these options. Generally, the options involving vessel conversion or charter or both (Options 4 and 5) will involve considerable lead time before field work can be conducted.

TUNA TAGGING IN THAILAND WATERS

During the past decade, Thailand has become the major canned tuna exporting nation in the world. In 1985, the production of canned tuna by Thailand was 10.9 million standard cases; 57% of the canned tuna was shipped to markets in the U.S.A. (Herrick 1986). Although the production sector of the Thailand tuna fishery has shown some growth, the major part of the supply for the canning industry has been through purchases from outside sources. The tuna fishery in Thailand increased steadily from 6.5 thousand mt landed in 1973 to 82.0 thousand mt in 1983; the 1984 landings showed a decline to 69.2 thousand mt (FAO 1986).

Tunas are caught in the Gulf of Thailand and along the west coast of Thailand by several types of gear; the principal gear types include drift gill nets and purse seines (Thai purse seine and the luring purse seine). Catches in 1984 were 26.4% and 70.3% for the two gear types, respectively (FAO 1986). About 85.8% of the Thailand tuna catch was taken from the Gulf of Thailand.

Longtail tuna, kawakawa, and frigate tuna are the principal tuna species taken by the various gear types; all three species are taken throughout the year. In 1979-81, exploratory cruises conducted by an FAO/UNDP project revealed the presence of skipjack tuna in commercial abundance off the west coast of Thailand (Lee 1982). A fishery for this species, however, is yet to be developed.

Objectives of a Tagging Program

A need exists for determining the dynamics of the longtail tuna resource in the Gulf of Thailand; however, tagging as a means to define the migratory pathways of the longtail tuna was not considered as a high priority research objective by Thailand. Instead, high priority was given to identifying the size of the skipjack tuna resource in the waters off the west coast of Thailand. Reference was drawn to the tagging study undertaken in 1977-1980 by the South Pacific Commission, which concluded that a large skipjack tuna resource existed in the central and western Pacific Ocean. The skipjack tuna resource in the SPC region was estimated to exceed 3.0 million metric tons (Kleiber 1983); the tagging data revealed a complex pattern of movement. Conceivably, the skipjack tuna resource in the eastern Indian Ocean is large and undergoes movement through waters of Indonesia, Malaysia, Thailand, and the Nicobar-Andaman Island regions. Although a well-designed, large-scale tagging program could aid materially in understanding this resource, a major drawback in initiating such an extensive tagging program at this time is the lack of wide-ranging fisheries for skipjack tuna in the eastern Indian Ocean. With the exception of coastal fisheries for skipjack tuna in western Indonesia, the only catches of skipjack tuna currently made in the region are from artisanal fisheries operating in near-coastal waters. The lack of extensive surface fisheries for tuna reduces the probability of successful recapture of tagged fish.

Although not covered under the terms of reference for this report, it would seem that some exploratory fishing would be more appropriate for the western Thailand region at this time.

Method of Tagging

The occurrence of adequate supplies of baitfish species suggests that a pole-and-line fishery, although not presently in existence in Thailand, would be the best method for a tagging program in the region for skipjack tuna or longtail tuna. In 1979, an FAO/UNDP project converted a commercial trawler to operate as a pole-and-line vessel (Lee 1982).

If this vessel is still available, the cost of implementing a tagging program will be reduced accordingly.

An alternative source of a fishing platform would be to charter one of the commercial tuna pole-and-line vessels operating in Indonesia. An earlier feasibility study of tuna tagging in the region (Gillett 1981) reported that the cost of chartering a 100-ton, commercial, pole-and-line vessel from the commercial fishery in Indonesia was about \$(US)25 thousand per month.

Should a decision be reached to undertake a tagging program restricted to the longtail tuna, an alternative to the pole-and-line method would be to tag fish from a trolling operation.

Number of Fish Expected to be Tagged

It would not be unreasonable to expect to tag 200-400 fish per fishing day if a suitable pole-and-line vessel is used for the tagging program. These estimates are based on the extensive tagging conducted in the eastern Pacific Ocean by IATTC and in the central and western Pacific by the SPC and various Japanese research agencies. Assuming 30 days of pole-and-line fishing during a 2-month tagging program, one can expect about 9,000 fish to be tagged.

If troll vessels are used to tag longtail tuna, the expected number of tuna tagged per day could range up to 100 fish per day. Assuming conditions of 1) 40 fishing days, 2) a daily catch of 75 viable fish for tagging, and 3) engaging three commercial troll vessels for the tagging program, the total number of fish projected for the proposed program is 9,000 longtail tuna.

Budget and Time Table

Table 5 provides an estimated cost of the several options described above, to implement a tagging program in the Thailand region. It should be noted that a tagging program for skipjack tuna or longtail tuna should include Malaysia and Indonesia.

A time table is provided in Figure 3, covering the several options described above.

TUNA TAGGING IN MALAYSIAN WATERS

Presently tuna represents only a small proportion of the total marine fish landings of Malaysia. In 1983, the total tuna landings were reported as about 19,000 mt: 16,000 mt from the fisheries based along the east coast of Peninsular Malaysia and about 3,000 mt from the fisheries based on the west coast (FAO 1986).

The principal methods used in tuna fishing include the drift gill nets and trolling gear; both gear types account for about 90% of the total tuna catch in Malaysia.

Similar to the tuna landings in Thailand, the principal species taken by the tuna fisheries of Malaysia are the longtail tuna and kawakawa. The two species make up about 99% of the tuna landings. Small amounts of frigate, skipjack, bullet, and oriental tunas also are landed.

Objectives of a Tagging Program

A high priority has been placed by Malaysia to define the migratory pathways of the longtail tuna in Malaysian waters and to determine the size of the resource. There is a need to determine whether this species moves into other areas of the Gulf or even into waters outside of the Gulf of Thailand; e.g., Indonesian waters.

Another area identified for a tagging experiment is the region around Sabah and Serawak, where skipjack and yellowfin tuna are taken by commercial fisheries. Until recently, a ring-net fishery using payaos operated off Sabah; however, the present status of this fishery is unknown.

Method of Tagging

Among the existing methods of tuna fishing currently used in Malaysia, trolling appears to be suitable for tagging the longtail tuna. Troll vessels are common along the east coast of Peninsular Malaysia, especially at Terengganu, which is one of the principal tuna landing ports. Troll vessels are reported to average about 500 kg of longtail tuna per trip during the peak season (June-August), each trip lasting about 5 days.

Because pole-and-line fishing is not used in Malaysia, an implementation of this technique for a tagging program will entail converting an existing fishing vessel into pole-and-line fishing or chartering a vessel from outside the region; e.g., Indonesia.

Number of Fish Expected to be Tagged

During a 2-month tagging period, a single tagging operation on a commercial troll vessel should tag about 2,500 fish. This assumes 1) an average catch of 500 kg longtail tuna, 2) an average size of longtail tuna of 1.2 kg, 3) about 75% of the catch being viable for tagging, and 4) making eight fishing trips during the 2-month period. It would not be unreasonable to project a three-vessel tagging operation based in Terengganu, thus, tagging about 7,500 longtail tuna.

Budget and Timetable

Table 6 provides budget estimates for the several options discussed above; Figure 4 provides a general time table for these options. As expected, the time needed to prepare for a tagging program involving a pole-and-line vessel will be considerably longer than making arrangements with commercial troll vessels.

BIBLIOGRAPHY

- Bayliff, W. H.
1973. Materials and methods for tagging purse seine-and-baitboat-caught tunas. Inter-Am. Trop. Tuna Comm., Bull. 15(6):463-503.
- Bayliff, W. H., and K. N. Holland.
1986. Materials and methods for tagging tuna and billfishes, recovering the tags, and handling the recapture data. FAO Fish. Tech. Pap. 279, 36 p.
- Collette, B. B., and C. E. Nauen.
1983. FAO species catalogue of tunas, mackerels, bonitos and related species known to date. FAO Fish. Synop. 125, vol. 2, 137 p.
- Food and Agriculture Organization of the United Nations.
1986. Yearbook of fishery statistics, 1985. FAO 60, 462 p.
- Gillett, R.
1981. Indonesia/Philippine tuna tagging programme. (FAO draft internal document.)
- Herrick, S. F., Jr., and S. J. Koplin.
1986. U.S. tuna trade summary, 1984. Mar. Fish. Rev. 48(3):28-37.
- Indo-Pacific Tuna Development and Management Programme.
1986. Report of the Meeting of Tuna Research Groups in the Southeast Asian Region, Phuket, Thailand, 27-29 August 1986. Indo-Pac. Tuna Dev. Manage. Prog., Colombo, Sri Lanka. IPTP/86/Gen/10, 75 p.
- Kearney, R. E.
1979. Skipjack survey and assessment programme. Annual report for the year ending 31 December 1978. South Pacific Commission, Noumea, New Caledonia, 15 p.
- Kearney, R. E. (editor).
1982. Methods used by the South Pacific Commission for the survey and assessment of skipjack and baitfish resources. Tuna and Billfish Assessment Programme, Tech. Rep. 7, 122 p. South Pacific Commission, Noumea, New Caledonia.
- Kleiber, P., A. W. Argue, and R. E. Kearney.
1983. Assessment of skipjack (Katsuwonus pelamis) resources in the central and western Pacific by estimating standing stock and components of population turnover from tagging data. Tuna and Billfish Assessment Program, Tech. Rep. 8. South Pacific Commission, Noumea, New Caledonia.
- Laurs, R. M., and J. A. Wetherall.
1981. Growth rates of North Pacific albacore, Thunnus alalunga, based on tag returns. Fish. Bull., U.S. 79(2):293-302.

Lee, R. E. K. D.

1978. Results of small scale live bait pole-and-line fishing explorations for tuna in the Philippines. South China Sea Fisheries Programme, Manila. SCS/78/WP/70, 41 p.

1982. A report prepared for the pole-and-line tuna fishing in southern Thailand Project. Fishing for tuna. FI: DP/THA/77/008, 73 p.

Marr, J. C.

1963. Note on the return rate of tagged skipjack, *Katsuwonus pelamis*, and the effects of handling. Int. Comm. Northwest Atl. Fish. Spec. Publ. 4:15-16.

Mather, P. J. III.

1962. Transatlantic migration of two large bluefin tuna. J. Cons. Cons. Int. Explor. Mer 27(3):325-327.

Queeneth, M. K. K., and R. W. Brill.

1983. Operations and procedures manual for visiting scientists at the Kewalo Research Facility. Natl. Mar. Fish. Ser., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Cent. Admin. Rep. H-83-7, 16 p.

Wilson, R. C.

1953. Tuna marking, a progress report. Calif. Fish Game 39(4): 429-442.

Yonemori, T., J. Uktolseja, and G. S. Merta.

1985. Tuna tagging in eastern Indonesian waters. Indo-Pac. Tuna Dev. Manage. Prog., Colombo, Sri Lanka. ITPP/85/WP/12, 19 p.

Figure 1. FAO statistical areas for the Pacific Ocean

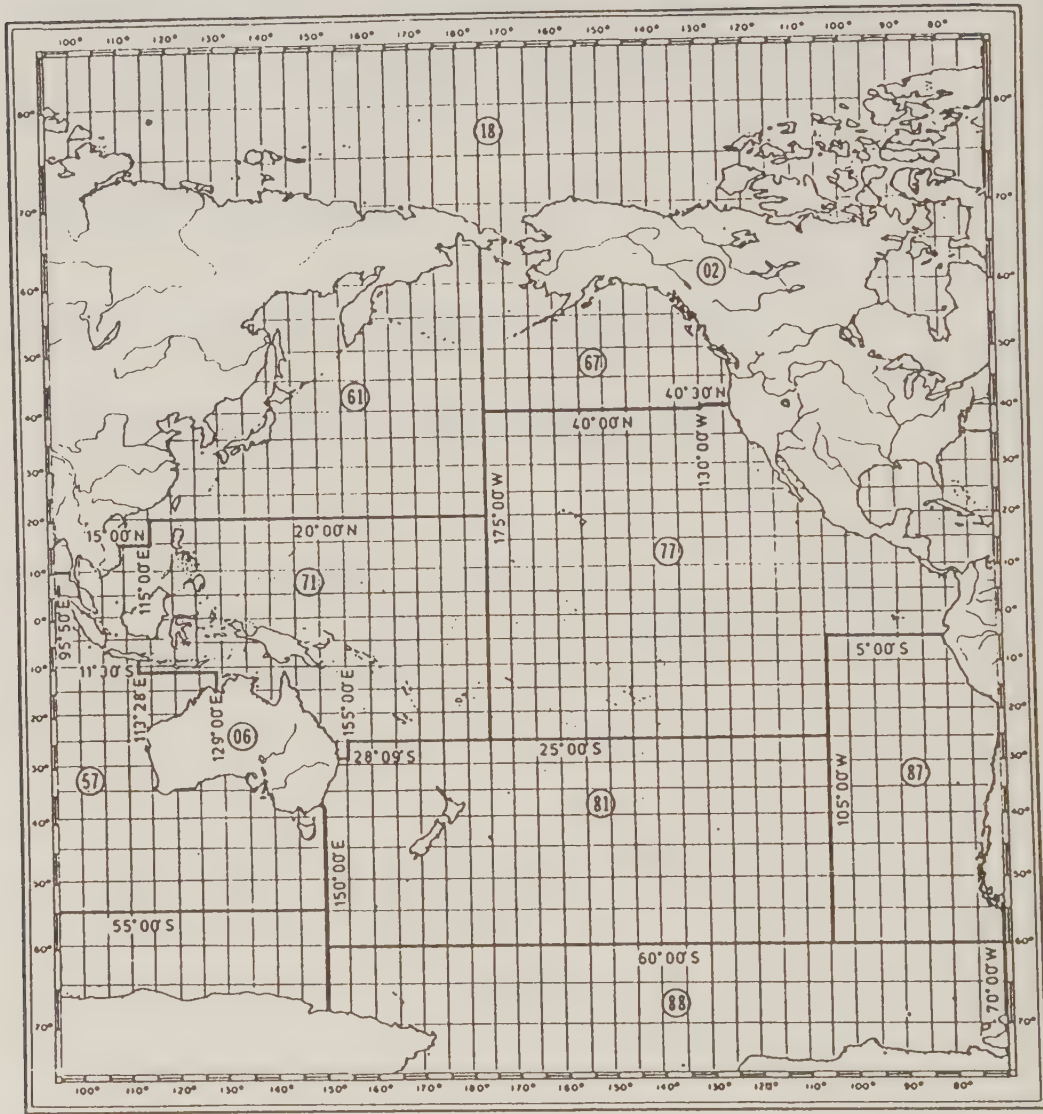


Table 1.—General evaluation of method of capture for tagging purposes.

Method	Potential large catch	Quality of fish	Size of fish
Pole-and-line	High	Good	Small-medium
Purse seine	Very high	Poor-medium	Small-large
Troll	Low-medium	Medium-good	Small-large
Gill net	Low-medium	Poor	Small-large
Longline	Low	Poor-Medium	Medium-large
Handline	Low	Good	Small-large

Table 2.—Recovery rates of tuna tagging experiments.

Area	Date	Agency	Type of tag	Method capture	Number tagged	Number recaptured	Recovery (%)
SKIRJACK TUNA							
HAWAII	1954-56	POFI	LOOP	P&L	742		0.6
HAWAII	1957	POFI	DART	P&L	8,161		9.2
PALAU	1968	POFI	DART	P&L	265	5	1.9
E. PAC.	1969(?)	IATTC	DART	PS	1,363	15	1.1
E. PAC.	1952-64	IATTC	DART	P&L	90,412	4,381	4.8
PNG		PNG	DART	P&L			14.0
FR. POL.	?	IATTC(?)	DART	P&L			0.3
CWPAC	19__-82	SPC	DART	P&L	ca.140,000		4.3
INDON	1983/84	I/IPTP	DART	P&L	378	1	0.3
INDO	1984	I/IPTP	DART	P&L	5,361	18	0.3
WPAC		JAPAN	DART	P&L			
ATLAN	1987	IOCAT	DART	?	2,264	125	5.5
YELLOWFIN TUNA							
E. PAC.	1969	IATTC	DART	PS	8,000		ca. 6.0
E. PAC.	1952-64	IATTC	DART	P&L	59,547	8,397	14.1
CWPAC	19__-82	SPC	DART	P&L			
INDO	1983	I/IPTP	DART	P&L	134	1	0.7
INDO	1984	I/IPTP	DART	P&L	575	1	0.2
WPAC	?	JAPAN	DART	P&L			
SOUTHERN BLUEFIN TUNA							
AUST	1983-84	AUST	DART	P&L(?)	ca.10,000	4,000	40.0
ALBACORE TUNA							
NPAC		NMFS	DART	TROLL			
NPAC		JAPAN	DART	P&L(?)			
SPAC		NMFS	DART	TROLL		2	
SPAC		ORSTOM	DART	TROLL			
SPAC		NZ	DART	TROLL			

Table 3.--Rewards for return of tuna tags.

South Pacific Commission

Tag return-- \$2.00 (local currency) or one T-shirt with tagging logo paid for each tag returned to SPC

Lottery----- annual lottery held with monetary prizes given for top 3 tag numbers randomly selected; prizes totaled \$2.0 thousand dollars (US)

AUSTRALIA

Tag return-- \$5.00 (A) paid for each tag returned

Lottery----- annual lottery held; prizes of \$400, \$600 and \$1,000 given to first three numbers randomly selected

ATLANTIC

Tag return-- \$5.00 (US) paid for each tag returned

Lottery----- annual lottery held; \$500 (US) for tropical tunas (yellowfin, bigeye and skipjack); \$500 (US) for temperate tunas (albacore and bluefin) and billfishes

U.S.A. (ALBACORE TUNA)

Tag return-- baseball cap with logo and \$2.00 (US) paid for each "standard" tag recovery; \$50.00 (US) paid for tag and fish (tetracycline injected fish); additionally, cannery price paid for fish

Lottery----- 3-5 drawings; cash awards (\$150-\$300 US) for first two winners; cases of tuna given to other winners

Table 4.—Budget estimate for tuna tagging in Philippine waters.

Object class (thousand US dollars)	Estimated cost	1	2	Options		3C	4	5
				3A	3B			
PERSONNEL								
Project Leader (8months)	1.0	X	X	X	X	X	X	X
Bio-tech (4mo)	0.8	X	X	X	X	X	X	X
Bio-tech (4mo)	0.8	X	X	X	X	X	X	X
Consultant (3 weeks)	4.2	X	X	X	X	X	X	X
Admin. support (host country)		X	X	X	X	X	X	X
Sea Duty stipend	3.2	X	X	X	X	X	X	X
TRAVEL								
Consultant	4.0	X	X	X	X	X	X	X
PL(domestic travel)	1.0	X	X	X	X	X	X	X
TAGGING PLATFORM								
Banca charter	?	X	0	X	0	0	0	0
P&L								
conversion	25.0	0	0	0	0	0	X	0
operating (3 mo)	45.0	0	0	0	0	0	X	0
charter	75.0	0	0	0	0	0	0	X
Ring-net owner	?	0	X	X	X	X	0	0
EQUIPMENT/SUPPLIES								
Tags (10,000)	5.0	X	X	X	X	X	X	X
Tagging needles (600)	1.2	X	X	X	X	X	X	X
Cradles (3)	0.3	X	X	X	X	X	X	X
Tape recorders(3)	0.3	X	X	X	X	X	X	X
Calipers(3)	0.3	X	X	X	X	X	X	X
Micro-computer	5.0	X	X	X	X	X	X	X
Holding pen	1.0	0	X	X	X	X	0	0
OTHERS								
Posters	0.2	X	X	X	X	X	X	X
Printed T-shirts	2.0	X	X	X	X	X	X	X
Lottery awards (3 yrs)	3.0	X	X	X	X	X	X	X
Data mgt	1.0	X	X	X	X	X	X	X
MISCELLANEOUS								
	4.0	X	X	X	X	X	X	X
TOTAL								

1/ X denotes item to be included in the option

0 denotes item not to be included in the option

Figure 2.—Projected timetable for tuna tagging program in Philippine waters.

Activity	1	2	3	4	5	6	7	8	9	10	11	12
	(months)											
1. Selection/appointment of Consultant and Project Leader (1 mo)			/	—	/							
2. Work out arrangements/ agreement with government (2 mo)			/	—	—	/						
3. Project preparation (includes arrangement for tagging platform, purchase equipment/supplies, posters, logbooks, develop data mgt system) (2 mo)			/	—	—	/						
4. Implementation of field work (2 mo)				/	—	/						
5. Analysis/write up of report (2 mo)					/	—	—	/				
6. Present results to Government and fishing industry (2 wks)							/	—	/			

Table 5.—Budget estimate for tuna tagging in Thailand waters.

Object class	Estimated cost (US dollars)	Pole-and-line convert charter		Troll	Purse seine
PERSONNEL					
Project Leader (8 mo)	2.9	X	X	X	X
Bio-tech (4mo)	1.0	X	X	X	X
Bio-tech (4mo)	1.0	X	X	X	X
Consultant	4.2	X	X	X	X
Admin. support	Host Country	X	X	X	X
Sea duty stipend (240 sea-days)	1.9	X	X	X	X
TRAVEL					
Consultant	4.0	X	X	X	X
Proj. Leader (domestic)	0.5	X	X	X	X
TAGGING PLATFORM					
Conversion	25.0	X	0	0	0
Operation (3mo)	45.0	X	0	0	0
Charter P&L (3mo)	75.0	0	X	0	0
Charter Troll (3vess.)	?	0	0	X	0
Purse seiner (RV CHULABORN 3mo)	60.0				
EQUIPMENT/SUPPLIES					
Tags (10,000)	5.0	X	X	X	X
Tagging needles (600)	1.2	X	X	X	X
Tagging cradles (3)	0.3	X	X	X	X
Calipers (3)	0.3	X	X	X	X
Micro-computer (1)	5.0	X	X	X	X
OTHERS					
Posters	0.2	X	X	X	X
Printed T-shirts (800)	2.0	X	X	X	X
Lottery awards (3yrs)	3.0	X	X	X	X
Data mgt	1.0	X	X	X	X
MISCELLANEOUS					
	4.0	X	X	X	X
TOTAL		-	-	-	-

1/ X denotes item to be included in the option

0 denotes item not to be included in the option

Figure 3.—Projected timetable for tuna tagging program in Thailand waters.

[illegible]

Table 6.--Budget estimate for tuna tagging in Malaysian waters.

Object class	Troll operation (Thousand US dollars)
PERSONNEL	
Project Leader (8 mo)	4.8
Bio-tech (4 mo)	1.4
Bio-tech (4 mo)	1.4
Bio-tech (4 mo)	1.4
Consultant (3 weeks)	4.2
Admin. support	Host country
Sea duty stipend	2.4
TRAVEL & PER DIEM	
Consultant	4.0
Project Leader (domestic travel)	0.5
TAGGING PLATFORM	
Usage costs (3 vessels)	9.6
Payment tagged fish (7,500)	6.0
EQUIPMENT/SUPPLIES	
Tags (10,000)	5.0
Tagging needles (600)	1.2
Tagging cradles (3)	0.3
Calipers (5)	0.5
Micro-computer (1)	5.0
OTHERS	
Posters	0.2
Printed T-shirts (800)	2.0
Lottery awards (3years)	3.0
Data mgt	1.0
MISCELLANEOUS	4.0
TOTAL	57.9

Figure 3.—Projected timetable for tuna tagging program in Malaysian waters.

Activity	1	2	3	4	5	6	7	8	9	10	11	12
	(months)											
1. Selection/appointment of Consultant and Project Leader (1 mo)			/..									
2. Work out arrangements/agreement with government (1.5 mo)			/....									
3. Work out arrangement for tagging platform (1 mo)			/..									
4. Preparation-purchase of equipment/supplies (2 mo)				/.....								
5. Conduct field work (2 mo)					/.....							
6. Analysis/write-up of results (2 mo)						/.....						
7. Present results to Government and fishing industry (2 wks)								/..				

Appendix Table A.—Meetings and consultations.

Several meetings and consultations were held during the consultant's visit of the Philippines, Thailand, and Malaysia. Individuals met included the following:

Philippines

Manila—(meeting in the conference room of BFAR on 10 August 1987)

Dr. Virginia Aprieto, College of Fisheries, Univ. Philippines
 Mrs. Aurora Reyes, BFAR
 Ms. Filomena Gande, Planning Officer, BFAR
 Mr. Reuben Ganaden, Chief, Fisheries Biology Section, BFAR
 Mr. Noel Barut, Biologist, BFAR

Note—also met briefly with Director Juanito Malig to inform him of the overall objectives of the project

General Santos—(meeting in BFAR regional office on 11 August 1987)

Mr. Expidito Respacia, SAFI
 Mr. Mario Mallorca, RS Albina Fishing Co.
 Ms. Minda L. Regidor, DFE Co.
 Mr. Eliseo Aguinaldo, Dela Pena Fishing Co.
 Mr. Rudy Rivera, RD Fishing Industry, Inc.
 Mr. Rene Kintanar, QBRO Fishing Co.
 Ms. K.L. Yamanaka, Univ. of British Columbia, Canada
 Mr. Eliseo Depra, Jr., Provincial Fisheries Officer, BFAR,
 General Santos Office
 Mr. Reuben Ganaden, BFAR
 Mr. Noel Barut, BFAR

Thailand (Bangkok)

Met with Mr. Boonlert Phasuk (Director, Marine Fisheries Division for the Government of Thailand) and Dr. Veravat Hongskul (Secretary-General, SEAFDEC) on 17 August 1987.

Malaysia (Penang)

Met with the following individuals at the Fisheries Research Institute:

Mr. ONG Kah Sin, Acting Director of Research (Fisheries Research Institute)
 Mr. LUI Yean Pong, Senior Fisheries Officer (Acting Head of Resources Section, Fisheries Research Institute)
 Mr. Abdul Hamid Yasin, Fisheries Officer, Branch of the Fisheries Research Institute, Kuala Terengganu
 Ms. CHEE, Phaik Ean, Fisheries Officer, Fisheries Research Institute

Pacific Billfish Angler Catch Rates for Key Area Stock Assessments

JAMES L. SQUIRE

Introduction

The catch per unit effort (CPUE) or other statistical measures of fishing effort and success are not well known for most Pacific big-game fisheries for billfishes (and also tunas). Nevertheless, assessments of the stocks involved concern both anglers and fishery managers confronted with interactions arising from commercial and recreational interests in these fisheries.

Fisheries agencies have long attempted to obtain data on billfish catch, effort, and biology from recreational fisheries. Data have been obtained from tournaments, voluntary logbooks programs, club records, observations of charterboat catches, individual angler records, and from special government monitoring programs. Some of this sampling has been successful, but in most cases quality of the statistics or sampling bias has been a problem (Abramson, 1963; Calhoun, 1950).

The sport fishery consists of many small and mobile units that may or may not land their billfish catches at locations where the record of the landing was made. The total annual recreational billfish catch and the effort expended in making this catch in the Pacific is unknown. The commercial longline, harpoon, and gillnet fleets of Japan, Korea, and Taiwan account for the major portion of billfish taken in the Pacific, and extensive data on landings in weight and numbers of fish, and locations of catch and hook effort expended are maintained by the fishing vessels for government agencies.

The purpose of this paper is to show that catch rates derived from localized recreational fisheries can be used to monitor stocks that are distributed widely and also commercially exploited. The center of distribution of such stocks, however, must be near the recreational fishery. Catch rates of billfish from recreational fisheries will be described and then compared with those from commercial fisheries.

The Angler Survey

Early west coast marine sport fishery surveys to determine total catch were conducted by the U.S. Fish and Wildlife Service through contract to the U.S. Department of Commerce, Census Bureau (Clark, 1960). They were inaccurate relative to billfish catch, as indicated by comparisons of the number of billfish caught off southern California with records from various billfish clubs. The Pacific Billfish Angler Survey was initiated to obtain a better measure of both

catch and angler effort from California and from other major billfish fishing areas in the Pacific Ocean. In recent years, angler response has been received from recreational fishing areas in the Indian Ocean and the survey has been expanded to include this area.

The U.S. Fish and Wildlife Service's Tiburon Marine Laboratory began the Pacific Billfish Angler Survey in 1969, and the survey was later transferred to the U.S. Department of Commerce's National Marine Fisheries Service (NMFS) in the National Oceanic and Atmospheric Administration. In an attempt to sample economically a large number of Pacific billfish anglers, the postcard type survey method was adopted. G. B. Talbot was the original designer of the postcard-type Pacific Billfish Angler Survey.

The postcard survey method of obtaining recreational fishery data has certain problems as reviewed by Abramson (1963) and Calhoun (1950). One problem is that it may be difficult for a fisherman to remember precisely the catch from the previous year. However, since the average billfish angler does not participate in the sport frequently, and since his catch is small and billfish are "trophy fish," his recall should be better than might be expected. The survey postcard format has changed considerably since 1969 (Squire, 1974). It has been simplified to encourage accurate and complete response (Fig. 1). Anglers are requested to give an honest answer and are told that information on zero catches was important. Despite its simple format, billfish anglers frequently make mistakes in completing the survey form.

The Pacific Billfish Angler Survey form is mailed annually with the NMFS Southwest Fisheries Center's *Billfish Newsletter*. The newsletter and angler survey form are sent to all anglers who

ABSTRACT—The Pacific Billfish Angler Survey was initiated in 1969 to measure the trend of angler CPUE annually. Survey respondents (1969-84) have reported 145,661 angler days catching 59,460 billfish, resulting in an average CPUE of 0.41 fish/day or 2.45 days of fishing per billfish. Annual totals of catch, effort, and resulting CPUE are given for many of the important recreational billfish fishing areas. A comparison of CPUE trends between the commercial longline and the recreational angler is made for the area about the southern tip of Baja California where high CPUE rates are common to both fisheries. The correlation between recreational and commercial CPUE is reasonable ($Y_2 = 0.82$), and the recreational angler CPUE is negatively affected by the nearby commercial longline fishery.

James L. Squire is with the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

Figure 1.—Pacific Billfish Angler Survey form.

have either tagged and released billfish, or who have returned an angler survey form for the preceding year. Billfish angler survey forms¹ are distributed during the spring months of the year following the year surveyed. Survey forms are collected for the preceding surveyed year through September. The forms are coded and the catch and effort data are placed in the SWFC computer facility, and are analyzed to determine the catch rates of the various fishing areas in the Pacific.

Estimates of catch and effort were made annually for the total Pacific and for specific fishing areas. Approximate fishing days reported by the billfish angler (f) are summed and divided into the total billfish catch reported (C):

$$\frac{C}{f} = \text{CPUE (catch per angler day)}.$$

Also, to determine the average amount of effort required by an angler to catch a billfish is calculated:

$$\frac{f}{C} = \text{EPUC (days fishing per billfish)}.$$

Additional analyses are made for each species and major fishing area using approximate fishing effort and catch by species.

Angler response to the survey has been high for southern California. Analysis indicates that at least 33 percent of the anglers catching striped marlin have reported. This estimate is based on the number of striped marlin reported by respondents compared to the total annual striped marlin catch off southern California as reported by the big-game angling clubs. Response level is also high for fishing off Baja California Sur, Mex. and around the Hawaiian Islands, but less so for other ports along the west coast of Mexico, Central and South America, and many other important billfish fishing areas in the Pacific. Anglers have responded with survey cards from 35 different fishing areas in the Pacific. The distribution of the fishing locations is shown in Figure 2.

PACIFIC INTERNATIONAL BILLFISH ANGLING SURVEY
FOR CALENDAR YEAR 1983

NOAA FORM 38-10 National Marine Fisheries Service In Cooperation with the International Game Fish Association OMB NO. 0681-0020

LOCATION	HOW MANY DAYS FISHED FOR BILLFISH BY QUARTER (1983 ONLY)				HOW MANY BILLFISH CAUGHT BY QUARTER (1983 ONLY)												"TALL FISH"			
					BLUE MARLIN				BLACK MARLIN				STRIPED MARLIN							
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4				
SOUTHERN CALIF.																				
Baja CALIFORNIA																				
GUAYMAS																				
MATILAN																				
SAN BLAS																				
MANZANILLO																				
ALAPULCO																				
LOS MUELLOS																				
COSTA RICA																				
PANAMA																				
ECUADOR																				
PERU																				
HAWAII																				
TAHITI																				
SAMOA																				
GUAM																				
NEW ZEALAND																				
NEW GUINEA																				
AUSTRALIA																				
MALAYSIA																				
JAPAN																				
THAILAND																				
OTHER																				

* If Shortbill Spearfish and Cobia By

NAME _____

STREET ADDRESS _____ CITY/TOWN _____

COUNTRY/STATE _____ ZIP OR MAILING CODE _____

Please Fill This Out



Figure 2.—Locations of billfish angler effort as indicated by survey response. Locations with 1,000 or more angler-days reported are indicated by a circle.

Table 1.—Angler catch rates for the total Pacific Ocean, 1969-83, all billfish species.

Year	Effort (in angler days)	Catch	
		No. of fish	Fish per day
1969	6,481	3,502	0.54
1970	6,569	3,779	0.58
1971	5,622	3,449	0.61
1972	6,899	3,511	0.51
1973	4,788	1,882	0.39
1974	9,635	3,475	0.36
1975	7,305	2,761	0.38
1976	8,591	2,918	0.34
1977	11,125	3,953	0.36
1978	14,453	3,906	0.27
1979	12,058	3,786	0.31
1980	14,100	5,506	0.39
1981	11,075	4,555	0.41
1982	8,782	4,418	0.50
1983	9,070	4,017	0.44
1984	9,108	4,024	0.41
Total	145,661	59,460	

Results of the Survey

About 80 percent of the survey cards sent with the SWFC's annual *Billfish Newsletter* were returned. The mailing list for the *Billfish Newsletter* is composed of anglers who have tagged and released billfish or who have participated in previous angler surveys. Some of the anglers who had not fished for billfish during the previous year return their cards so that they can remain on the newsletter mailing list. The combined totals of the catch and effort sample for billfish fishing in the Pacific Ocean for the period 1969-84 is 145,661 angler days (average 9,103 days/year) reporting a catch of 59,460 billfish (all species combined). This is a CPUE of about 0.41 fish per day or 2.45 days per billfish. The highest CPUE, 0.58 fish/day, was recorded in 1970, and the lowest, 0.27 fish/day, was recorded in 1979.

The annual totals of catch, effort, and CPUE are given by year in Table 1. For fishing areas having 1,000 angler days reported, the angler effort, catch by species, and CPUE are given for 1969-83 in Table 2. These areas are southern California (U.S.); Baja California Sur, Guaymas/Pta. Penasco/Kino, Mazatlán, and Acapulco/Zihuatanejo/Ixtapa (Mex.); Australia; Hawaiian Islands; Panama; Ecuador; Costa Rica; and New Zealand. Statistics for locations having a respon-

dent level of less than 1,000 angler days are summarized in Table 3.

Striped Marlin

Some of the more productive recreational fishing grounds for striped marlin, *Tetrapturus audax*, in the Pacific Ocean are the areas around the southern tip of Baja California and off the coast of Ecuador. These waters are also fished for blue marlin, *Makaira nigricans*; black marlin, *M. indica*; and sailfish, *Istiophorus platypterus*. A commercial longline fishery targets on striped marlin and swordfish, *Xiphias gladius*; off Baja California Sur near the recreational fishery area. This commercial fishery has produced some of the highest catch rates for striped marlin recorded in the Pacific or Indian Oceans.

Striped marlin catch rates for recreational fisheries off Baja California Sur and Mazatlán, Mex. and off Ecuador, New Zealand, southern California, and the Hawaiian Islands are shown in Figure 3. These areas had effort rates greater than 2,000 angler days during 1969-83.

The recreational fishing area around the southern tip of Baja California Sur is located near a center of high striped marlin availability in the northeast Pacific, an area that accounts for most of the recreational catch of striped marlin in the eastern Pacific. For that reason, changes in catch rate in this area are of interest to

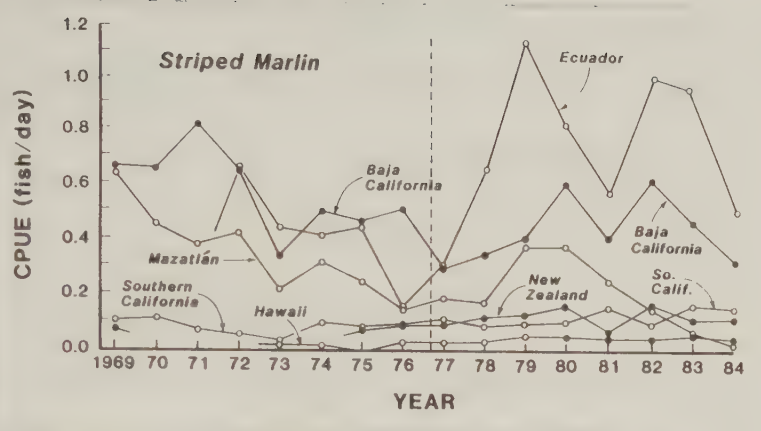


Figure 3.—Catch rates for striped marlin in areas having greater than 2,000 angler days.

recreational anglers, and to charterboat, fishing boat, and fishing resort operators. Catch rates declined in this area from about 0.66 fish per angler day observed during 1969-70 to 0.29 fish per day in 1977. This downward trend was reversed after 1977, and catch rates increased during 1978, 1979, and 1980 to 0.61, and then fluctuated between 0.41 and 0.62 from 1981 to 1983, declining to 0.32 in 1984 (Fig. 3).

Before the start of the Billfish Angler Survey in 1969, historical catch data obtained from the fishing resort of Rancho Buena Vista, located on Las Palmas Bay off the east coast of the southern tip of Baja California Sur, indicated a catch rate in the early 1960's of 0.6 to 0.9 striped marlin per angler day; the decline in the catch rate there from an estimated average of 0.75 in the early mid 1960's to about 0.30 fish per day in 1977 was substantial.

The average CPUE for striped marlin catches off Ecuador for 1978-84 was 0.83 fish per day, close to twice the rate of 0.46 fish per day recorded for Baja California Sur for the same period. The peak CPUE rates were also much higher, near 1.20 fish per day in 1978. However, the number of angler days reported was only 5 percent of that reported for Baja California Sur, making the Ecuador data less precise.

Striped marlin is the major billfish species reported from off Japan, and survey data were recently obtained from that

Table 2.—Reported catch, effort, and resulting CPUE rates for all locations in the Pacific having more than 1,000 angler days reported.

Location and year	Angler days	No. of billfish	Fish/ day	Days/ fish	Major species	Catch			Major species	Days/ fish	No. of billfish	Fish/ day	Days/ fish	Catch			
						Blue marlin	Striped marlin	Black marlin						Blue marlin	Striped marlin	Black marlin	
Southern California																	
1969	2,297	220	0.095	10.44	SM		220				1,971	0.78	1.28	SM	1,657		314
1970	2,068	232	0.11	8.91	SM		221				2,615	0.77	1.30	SM			357
1971	2,093	192	0.90	10.90	SM		152				2,793	0.91	1.10	SM	2,258		293
1972	2,212	119	0.05	18.59	SM		119				2,454	0.71	1.40	SM	2,207		244
1973	1,900	56	0.03	33.93	SM	10	46				790	0.44	2.28	SM	67	31	92
1974	4,409	460	0.10	9.58	SM	2	450	8			1,585	0.60	1.67	SM	600	6	206
1975	2,678	247	0.09	10.80	SM	3	238	6			2,239	0.56	1.80	SM	35	1,058	129
1976	2,848	275	0.10	10.36	SM		265	10			1,188	0.67	1.49	SM	47	897	14
1977	3,383	381	0.11	8.88	SM	6	358	17			2,186	0.40	2.48	SM	39	643	10
1978	5,684	429	0.08	13.25	SM	25	398	4			2,551	0.43	2.32	SM	58	855	6
1979	4,921	438	0.09	11.24	SM	7	399	17			1,099	0.49	2.03	SM	88	1,175	8
1980	3,900	429	0.11	9.09	SM	18	403	1			2,432	0.69	1.45	SM	91	2,143	20
1981	2,997	453	0.15	6.62	SM	16	428	2			2,000	0.47	2.11	SM	94	1,722	25
1982	2,666	296	0.11	9.01	SM	9	279				2,215	0.79	1.27	SM	129	1,735	22
1983	2,696	485	0.18	5.56	SM	27	450	8			2,049	0.73	1.37	SM	500	1,307	321
1984	2,874	397	0.14	7.49	SM	10	377	6			1,044	0.51	1.95	SM	203	659	7
Total	49,626	5,109	0.10	9.71	SM	133	4,803	25			27,520	0.63	1.58	SM	1,417	22,476	3,418
Hawaii																	
1969					BLM	30					398	0.53	1.90	BKLM		236	162
1970					BLM						69	0.30	3.32	BKLM		59	10
1971	77	30	0.39	2.57	BLM	76	1				157	0.44	2.27	BKLM		157	
1972	186	78	0.42	2.38	BLM	10					347	0.84	1.19	BKLM		347	
1973	84	12	0.14	7.00	BLM	88		1			543	0.88	1.33	BKLM	1	472	2
1974	1,003	100	0.10	10.03	BLM	12					540	0.61	1.65	BKLM	17	540	3
1975	1,677	77	0.11	8.79	BLM	76					689	0.61	1.23	BKLM	4	326	1
1976	1,826	201	0.11	9.08	BLM	146		5			706	0.88	1.14	BKLM	4	611	7
1977	1,984	432	0.22	4.59	BLM	245		8			1,036	0.52	1.92	BKLM	1	25	5
1978	2,926	598	0.20	4.89	BLM	465		13			574	0.56	1.80	BKLM	2	501	23
1979	2,017	721	0.22	4.57	BLM	315		20			601	0.54	1.86	BKLM	2	296	17
1980	3,652	721	0.20	5.07	BLM	483		76			503	0.43	2.34	BKLM	4	540	53
1981	1,448	327	0.23	4.43	BLM	248		146			662	0.58	1.74	BKLM	3	52	19
1982	953	248	0.26	3.84	BLM	180		44			381	0.63	1.59	BKLM	9	135	63
1983	1,377	361	0.26	3.81	BLM	264		6			353	0.63	1.59	BKLM	3	310	42
1984	1,435	357	0.25	4.02	BLM	250		11			471	0.53	1.88	BKLM	5	310	61
Total	19,645	3,983	0.20	4.93	BLM	2,976	562	6			6,257	0.63	1.59	BKLM	2	1	468
Panama																	
1969	26	24	0.92	1.08	SF						704	1.21	0.83	SM	382		322
1970	115	76	0.66	1.51	SF						588	1.28	0.78	SF	214		374
1971					SF						305	1.12	0.89	SF	101		204
1972	193	131	0.68	1.47	SF						188	0.64	1.56	SF	123		177
1973	157	159	1.05	0.96	SF						184	0.97	1.03	SF	61		121
1974	304	348	1.14	0.87	SF						125	0.89	0.92	SF	7	58	94
1975	167	279	1.31	0.75	SF						140	1.09	0.92	SF	1	29	1
1976	293	235	0.80	1.25	SF						114	0.83	1.07	SF	5	114	94
1977	377	288	0.76	1.31	SF						118	0.79	1.26	SF	2	29	86
1978	340	325	0.96	1.05	SF						111	0.91	1.96	SF	1	38	70
1979	347	265	0.76	1.31	SF						104	0.83	1.20	SF	3	38	2
1980	418	353	0.84	1.18	SF						141	0.98	1.02	SF	17	48	1
1981	455	457	1.00	1.00	SF						136	0.83	1.03	SF	3	54	1
1982	417	554	1.33	0.75	SF						63	0.64	1.57	SF	34	2	77
1983	178	82	0.46	2.17	SF						64	0.58	1.72	SF	3	15	45
1984	243	364	1.50	0.67	SF						8	0.71	1.41	SF	8	2	46
Total	4,025	3,860	1.04	0.96	SF						3,312	0.97	1.03	SF	1	13	2,021

Continued on next page.

Table 2.—Continued. Reported catch, effort, and resulting CPUE rates for all locations in the Pacific having more than 1,000 angler days reported.

Location and year	Angler days	No. of billfish	Fish day	Days fish	Major species	Catch				Days/ fish	Major species	Catch			
						Blue marlin	Striped marlin	Black marlin	Sailfish			Blue marlin	Striped marlin	Black marlin	Sailfish
New Zealand															
1969															
1970	41	3	0.07	13.67	SF		3				M		56		12
1971											M		75		4
1972	15	1	0.07	15.00	BKLM										
1973	8	0									SM				
1974	5	2	0.40	2.50	BLM	2							16		4
1975	146	74	0.51	1.97	BKLM	4					SM	1	28		19
1976	36	3	0.08	12.00	SM		10	60			SF		79		42
1977	191	17	0.09	11.24	SM		3				SF	2	48		75
1978	320	35	0.11	9.14	SM		16		1		SF	2	35		139
1979	169	21	0.12	8.05	SM		35				SM	2	66		42
1980	273	42	0.15	6.50	SM		19	2			SF	1	61		64
1981	457	39	0.09	11.72	SM	1	40				SM	1	192		12
1982	297	46	0.15	6.46	SM	6	30	2			SM	5	248		33
1983	631	79	0.13	7.99	SM	1	45				SM	4	137		7
1984	473	50	0.11	9.46	SM	7	68	2			SM	13	163		16
Total	3,062	412	0.13	7.43	SM	27	307	72	6		SM	19	144	15	24
Acapulco-Zihuatanejo-Ixtapa															
1969	112	111	0.94	1.05	SF		5								
1970	97	84	0.87	1.15	SF		9								
1971	40	42	1.05	0.95	SF		2								
1972	64	44	0.69	1.45	SF		3								
1973	30	35	1.17	0.85	SF		10				SF				
1974	42	53	1.26	0.79	SF		1								
1975	106	71	0.67	1.49	SF		12								1
1976	96	150	1.56	0.64	SF		59				SF				85
1977	314	456	1.45	0.69	SF		3	1			SF				100
1978	114	100	0.88	1.14	SF		6	1			SF	1	1		457
1979	227	218	0.96	1.04	SF		5				SF				62
1980	69	81	1.17	0.85	SF		5				SF	3	5		129
1981	105	122	1.12	0.89	SF		1				SF	5	5		185
1982	46	44	0.96	1.05	SF						SF	2	29		4
1983	100	87	0.87	1.15	SF	1	2	1			SF	4	5	15	223
1984	78	62	1.26	0.79	SF	4					SF	6	8	238	
Total	1,644	1,760	1.07	0.93	SF	5	64	5	1,686			25	50	17	279
Guaymas-Kino/Pta. Penasco															
1969															
1970															
1971	67	50	0.75	1.34	SF						SF				16
1972	64	17	0.27	3.76	SF						SF				37
1973	38	20	0.53	1.90	SF						SF				7
1974	53	24	0.02	2.21	SF		2				SF	1	12		14
1975	143	34	0.24	4.21	SF						SF				3
1976	100	40	0.42	2.38	SF	1	4				SF		1		7
1977	86	16	0.19	5.38	SF						SF				30
Total												2	25		309
Guaymas-Kino/Pta. Penasco															
1969															
1970															
1971															
1972															
1973															
1974															
1975															
1976															
1977															
Total															
Costa Rica															
1969															
1970															
1971															
1972															
1973															
1974															
1975															
1976															
1977															
1978															
1979															
1980															
1981															
1982															
1983															
1984															
Total															
Guaymas-Kino/Pta. Penasco															
1969															
1970															
1971															
1972															
1973															
1974															
1975															
1976															
1977															
Total															
Ecuador															
1969															
1970															
1971															
1972															
1973															
1974															
1975															
1976															
1977															
1978															
1979															
1980															
1981															
1982															
1983															
1984															
Total															
Guaymas-Kino/Pta. Penasco															
1969															
1970															
1971															
1972															
1973															
1974															
1975															
1976															
1977															
Total															
Costa Rica															
1969															
1970															
1971															
1972															
1973															
1974															
1975															
1976															
1977															
1978															
1979															
1980															
1981															
1982															
1983															
1984															
Total															
Guaymas-Kino/Pta. Penasco															
1969															
1970															
1971															
1972															
1973															
1974															
1975															
1976															
1977															
Total															
Costa Rica															
1969															
1970															
1971															
1972															
1973															
1974															
1975															
1976															
1977															
1978															
1979															
1980															
1981															
1982															
1983															

Table 3.—Reported catch, effort and resulting CPUE rates for locations having a response level of less than 1,000 angler days.

Location	Angler days	No. of billfish	Fish/day	Days/fish	Major species
Manzanillo, Mex.	928	595	0.64	1.56	SF
Thailand	522	243	0.47	2.15	BKLM
Guatemala	435	178	0.41	2.44	SF
Tahiti	434	124	0.29	3.50	BLM
New Guinea	386	92	0.24	4.20	SF
San Blas, Mex.	320	224	0.70	1.43	SF
Guam	265	45	0.17	5.89	BLM
Fiji	159	9	0.06	17.67	SF
Philippine Islands	122	37	0.30	3.30	SF
Samoa	93	10	0.11	9.30	BLM
Puerto Vallarta, Mex.	90	52	0.58	1.73	SF
Peru	38	9	0.28	4.22	SM
Japan	78	38	0.43	2.05	SM
Clipperton Island	23	1	0.04	23.00	SF
Columbia	34	33	0.97	1.03	SF
Marshall Islands	18	4	0.22	4.50	BLM
Revillagigedo Islands	18	3	0.17	6.00	SM
New Caledonia	12	0			
Nicaragua	2	8	4.00	0.25	SF
Yap Island	7	1	0.14	7.00	BLM
Topolobampo, Mex.	7	3	0.43	2.33	SF
El Salvador	6	6	1.00	1.00	SF
Palau	6	2	0.33	3.00	BKLM/SF
Borneo	4	1	0.25	4.00	BKLM
Chile	3	0			
Cook Island	4	0			
China	3	0			

fishery. From data obtained in 1982 and 1983, the catch rate was 0.49 striped marlin per angler day, only slightly less than the 1981-83 average of about 0.53 fish per day for Baja California Sur.

Environmental changes can have a significant impact on CPUE rates by modifying the distribution and behavior of the fish. The years of 1982-83 was an El Niño period of warmer sea surface temperature in the eastern Pacific. The effect of this environmental change was evident from the change in abundance/availability of several billfish species around the southern tip of the Baja California peninsula. Striped marlin CPUE dropped from the 1982 level of 0.62 fish per day to 0.47 in 1983 and to 0.32 fish per day in 1984. Though striped marlin had become less abundant around the tip of Baja California, a joint-venture Mexican/Japanese commercial longliner operation working to the west and southwest of the southern tip of Baja California (Cabo San Lucas) did obtain CPUE rates comparable to those of previous years. Blue marlin CPUE increased substantially during the El Niño of 1983 from an average of 0.03 fish per day (1973-82) to 0.18 fish per day in 1983 and continued at a rate of 0.10 in 1984. In 1983 and 1984 the center of the California catch correspondingly

shifted to the northwest between San Nicolas Island and the Santa Barbara Channel Islands. This area is northwest of the normal catch areas around Catalina Island, between Catalina Island and the mainland, and off San Diego. Sea surface temperatures were very warm off southern California during the 1983 El Niño and were higher in 1984; catches of striped marlin increased with a record of CPUE rate of 0.16 fish per day in 1983 and 0.13 fish per day in 1984. These increases were related to above average sea surface temperatures off the northwest coast of Baja California and southern California (Squire, 1974).

Blue Marlin

Blue marlin is common to tropical oceans and is a dominant billfish species in the central Pacific area from the Tuamotu Islands in the southeast to the Marianas Islands in the northwest. These areas appear to be the major habitat of blue marlin. Commercial longline catches of this species declined in the Pacific to about 12,500 metric tons (t) in 1975, but since 1975 catches have increased.

Angler catch rates for blue marlin are normally lower than those observed for striped marlin and sailfish (Fig. 4). However, the size of this species (up to 2,000 pounds-plus) makes it an attractive sportfish. Limited survey data from Tahiti and Guam show CPUE rates that are not substantially different from those of Hawaii. CPUE rates ranged from 0.16 to 0.28 fish per day in 1984.

Angler response from Hawaii was high compared with that of other island areas in the central Pacific. In 1970 and 1972 Hawaiian catch rates for blue marlin were considerably higher than in 1973-83; however, the sample size in the early 1970's was small compared with that of later years. Blue marlin catch rates have increased from about 0.10 fish per day during 1973-76 to nearly 0.25 fish per day in 1984.

Although the angler response rate is low for the Tahiti areas, data collected since 1976 indicate an average CPUE rate of 0.23 fish per day. This is above the Hawaiian Islands average of 0.18 fish per day for the same period. The CPUE

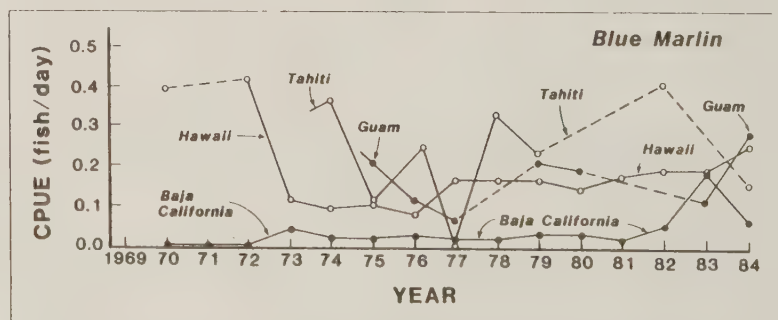


Figure 4.—Catch rates for blue marlin in areas having a response rate of greater than 200 angler days.

rate for blue marlin caught off Baja California Sur is usually very low (0.03 fish per day average), except for the El Niño years of 1982-83 when the CPUE rate increased to 0.18 fish per day, a CPUE similar to that observed for the central Pacific Ocean.

Black Marlin

The center of black marlin distribution is in the southwest Pacific and Indo-Pacific area. High angler CPUE rates were recorded for the area along the Great Barrier Reef, Queensland, Australia, located on the western edge of the Coral Sea. Angler catch rates for black marlin in areas having a response rate greater than 200 angler days are shown in Figure 5.

Large fluctuations in catch rates for black marlin were observed off Queensland during the early years of the survey (Fig. 5). High catch rates of up to 1.5 fish per angler day were observed in 1971 and 1973. The rates declined to a level of about 0.5 fish per day in 1978 and since then remained near that level. The average CPUE for 1976-84 is 0.54. This fishery produces large fish and many of the catches are in excess of 300-400 pounds. Considering that the CPUE is about 0.5 fish per day, the catch per angler in weight is one of the highest in the world. Thailand reported an angler CPUE rate of 0.44 fish per day, only slightly less than that observed for the Queensland area; however, the fish caught off Thailand were not as large as those caught off Queensland, Australia (pers. commun.). In the eastern Pacific Ocean some black marlin are landed in the tropics off Central and South America, and billfish anglers fishing in Panama report an average CPUE rate of 0.11 fish per day.

Sailfish

High commercial and recreational CPUE rates for sailfish are observed along the eastern Pacific coast from Panama to the Gulf of California, Mex. This area has the highest abundance of sailfish in the eastern Pacific. Abundance is highest along the coast from near Acapulco, Mex., south to off Costa Rica and Panama during the winter. In the spring and summer, sailfish move northward

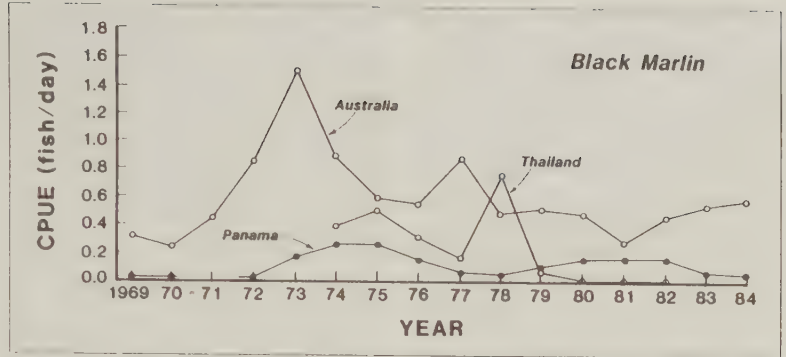


Figure 5.—Catch rates for black marlin in areas having a response rate of greater than 500 angler days.

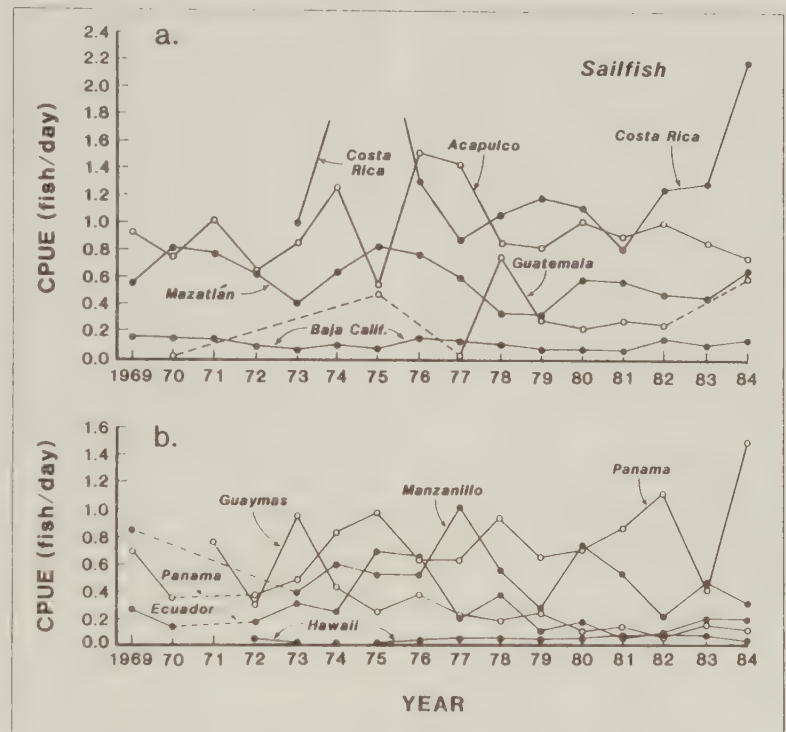


Figure 6.—Sailfish catch rates for areas (a and b) having a response of greater than 400 angler days.

and have been recorded in the northern part of the Gulf of California (lat. 31°N). The number of survey responses is low for anglers fishing in areas of high sailfish catches. Catch rates for Costa Rica, Guatemala, Mexico (Baja California Sur, Mazatlán, Manzanillo, Guaymas/Pta. Penasco/Kino, and a Acapulco/

Ixtapa), Ecuador, and Hawaiian areas as well are given in Figure 6a-b. These areas have substantial catches of sailfish and an angler response rate of 400 or more angler days. The CPUE rate for fishing off Acapulco/Ixtapa, Mex., an area near the center of Pacific sailfish distribution, averages about 1.0 fish per

day. Costa Rica appears to have the highest sailfish CPUE in Central America; its CPUE reached 2.17 fish per angler day in 1984. Mazatlán, Mex., to the northwest has a catch rate that fluctuates around 0.5 fish per day with highs of 0.81-0.82 fish per day observed in 1970 and 1975. The ranges for sailfish catch rates for the southern tip of Baja California Sur are lower than those for Mazatlán and appear to be relatively stable at 0.08 fish per day. To the southwest, Manzanillo, Mex., and Panama have sailfish CPUE rates of 0.50-0.80 fish per angler day. CPUE rates below 0.50 were recorded from Guatemala, Ecuador, Baja California, Guaymas/Pta. Penasco/Kino, and the Hawaiian Islands.

The sailfish was one of the target species for the Japanese longline fleet operating off Mexico in the early years of that fishery (1960-65). In the eastern Pacific Ocean, catches were recorded in excess of 9,000 t in 1965. Catches then declined to about 3,500 t in 1975, increased to over 10,000 t in 1976, and then declined to a record low of less than 1,000 t in 1981. Annual CPUE rates of 90 fish per 1,000 hooks fished were recorded for some 5° long. × 5° lat. areas off Central America during the early years of the longline fishery.

Summary and Discussion

CPUE Trends From Billfish Survey and Recreational Fishery Data

Data on catch and effort for most recreational billfish fisheries in the Pacific Ocean are very limited. Therefore, the opportunities to compare the results of the postcard survey method with catch rates developed by other methods are few. Although some fishing resort operations maintain fishing records, these records are in most cases insufficient for generating CPUE values comparable to the records of the Billfish Angler Survey. Records for the resorts are maintained in "numbers of boat days," which poses the problem of the number of angler days actually represented. Charter boats may at times fish for species other than billfish, and this could result in CPUE error. In some areas (Baja

California), a substantial amount of angler response to the Billfish Survey is from U.S. fishermen who fish off private boats, and the catch rate for this private fleet may have a higher CPUE rate than the public charter boat fleet. Bias may also result if respondents to this survey are the more successful anglers.

Eastern Pacific

Some data suitable for comparison with the Survey CPUE rates off the Americas are available. From March 1978 to February 1979, biologist Hector Zurita Brito of Mexico's Departamento de Pesca conducted a comprehensive sampling study of the recreational billfish fishery in the Acapulco/Zihuatanejo area. About 30,000 sailfish were caught in this area annually and the catch rate was found to be 1.0 fish per day (Zurita Brito 1980, 1985). From the Billfish Angler Survey for the same area in 1978 the catch rate for sailfish was 0.87 sailfish per day. There was thus a 13 percent difference, or 0.13 fish per day less for Billfish Angler Survey data.

A field sampling program for billfish was conducted in 1968 and 1969 by the U.S. Fish and Wildlife Service in the Las Palmas Bay area of Baja California Sur (Rancho Buena Vista), and at Mazatlán. Results of this study are given in graphs in a paper by Talbot and Wares (1975). The following results were determined from the graphs to indicate the angler CPUE rates for striped marlin and sailfish off Bahia de Palmas (Baja California Sur) and Mazatlán.

Billfish Angler Survey, 1969 (first year of Survey).

	Talbot and Wares (1975)	Billfish Angler Survey
Striped marlin		
Mazatlán	0.45	0.66
Baja Calif.	0.60	0.66
Sailfish		
Mazatlán	0.60	0.55
Baja Calif.	0.10	0.12

A limited amount of catch/effort data from a leading fishing resort in the East Cape area of Baja California, located on Bahia de Palmas, was made available; analysis of these data indicate a striped marlin CPUE rate much lower than that recorded by the Survey:

Year	Billfish Angler Survey CPUE	Fishing Resort CPUE
1981	0.41	0.13
1982	0.62	0.16
1983	0.47	0.22 (first half year)

For Ecuador, fishing resort data had boat days only. The CPUE calculated using an estimated angler days effort (boat days multiplied by two) appeared more compatible with data from the Billfish Angler Survey than were sample data from Baja California:

Year	Billfish Angler Survey CPUE	Fishing Resort CPUE
1972	0.53	0.64
1973	0.35	0.43
1974	0.29	0.41

Angler catch rates for striped marlin at both locations appear not to be comparable with catch rates from the Billfish Angler Survey. Ecuador resort data, even though they were from a much smaller sample than the Baja California survey data (2,070 angler days vs. 41,534 angler days), were in better agreement with the Survey than the Baja California resort data.

Central and Western Pacific

Recent studies of the Hawaiian Island billfish fisheries provide a source of comparative data. Holland (1985) reported that by examining the number of marlin flags on charterboats entering Kewalo Basin, Honolulu, Hawaii, he was able to determine the number of marlin caught by this fleet. A measure of effort for full-day charters from the Kewalo Basin fleet indicated that the CPUE rate was one marlin per 6.25 days of fishing or 0.16 fish per boat day. On the other hand, Samples et al.¹, from economic survey data, reported that the 119 charterboats around the Hawaiian Islands fished an average of 155 trips per year catching an average of 47 billfish (striped, blue, and black marlin, sailfish, swordfish, and shortbill spearfish, *Tetrapturus angustirostris*). From this figure the total

¹Samples, K. C., J. Kusakabe, and J. Sproul. 1984. A description and economic appraisal of charterboat fishing in Hawaii. NMFS Honolulu Lab. Admin. Rep. H-84-6C, 130 p.

catch would be 5,593 billfish, reported to be taken by a total of 73,780 anglers, given a statewide CPUE of 0.08 billfish per angler day.

These surveys, however, do not indicate the charterboat trips that fished marlin as one of 13 groups of targeted fishes. From Samples et al.¹ data for the island of Hawaii, which has a higher percentage (14.8 percent) of billfish in the charterboat catch than the data from the islands of Oahu or Maui, the billfish CPUE rate (based on 128 days fishing per charterboat, a catch of 58 billfish, and an estimated three anglers per trip) is calculated to be 0.15 billfish per angler day. The Pacific Billfish Angler Survey CPUE for the Hawaiian Islands for 1978-84 is 0.13-0.19 fish per angler day with an overall average of 0.16 fish per angler day, which is comparable to the rates reported by Holland (1985) (though the Survey rates were higher than his during 1982-83) and by Samples et al.¹ The Billfish Angler Survey form does not separate response data by island.

Sample heterogeneity must account for much of the CPUE differences during comparable years. The Samples et al.¹ data represent findings from a statewide questionnaire; Holland's data are from the fishing grounds off the island of Oahu, not the best marlin fishing area in the Hawaiian Islands (Holland, 1985). The highest catch rates are recorded off the Kona coast of the island of Hawaii (Samples et al.¹), and the CPUE rates there are most like to those determined by the Billfish Angler Survey. The Billfish Angler Survey should be biased toward higher CPUE values because the respondent base is made up of anglers who are active in billfish fishing and who fish the higher density areas of billfish; it is possible that the better billfish anglers are primarily responding. Hawaiian angler catch rates of blue marlin, the major target species in the Hawaiian Islands area, are not as high as those observed for striped marlin and black marlin in other important recreational fishing areas. This is probably because the Hawaiian Islands are not geographically near the center of distribution for blue marlin while that is the case for the recreational fisheries for striped marlin about the tip of Baja California Sur and for black marlin near

the Great Barrier Reef off Queensland (Suzuki and Honma²). The distribution of blue marlin in the Pacific Ocean is centered in the south central Pacific Ocean (lat. 10°-20°S × long. 140°-160°N) from December to February and in the northwest central Pacific (long. 120°E) from June to August.

Catch rates for recreational billfish fisheries in most areas of the Pacific Ocean are relatively stable compared with the trend of catch rates observed for striped marlin about the southern tip of Baja California Sur, and for black marlin off the Queensland coast. Both of these productive recreational fishing areas are located near commercial longline fisheries that targets on these species. In summary, it appears that CPUE's derived from the Billfish Angler Survey are comparable to other angler surveys unless there are sampling errors.

Comparison of CPUE Trends Between the Commercial Longline and Recreational Fisheries

I compared the trends in CPUE's between geographical areas, such as off Baja California Sur and Queensland, which have both an intensive recreational fishing (high angler response) and a commercial longline fishery (high CPUE) for billfish species.

Black Marlin

Black marlin have been fished in the Coral Sea and other areas in the southwest Pacific by longline fleets from Japan since the early 1950's. The total number of black marlin caught by the Japanese commercial longline fleet in the southwest Pacific ranged from 4,000 to 14,000 fish per year during 1969-80. During this same period, CPUE rates calculated by 3-year periods indicate a decline from an average of 0.17 fish per 1,000 hooks (1969-71) to 0.07 fish per 1,000 hooks (1978-80) a 57 percent decline in CPUE (Anonymous, 1980).

Angler catch rates for black marlin off

Australia peaked in 1973 at about 1.5 fish per angler day. This peak may have been due to fleet expansion to new grounds and increased efficiency of the charter fleet during the early 1970's when the recreational black marlin fishery was developing rapidly off the Cairns area and also north of that area. The angler CPUE average for the 1971-75 period, 0.83, declined to 0.46 fish per angler day for 1979-1984, a 45 percent decline in angler CPUE. The commercial longline CPUE for the southwestern Pacific for 1972-74 was 0.11 fish per 1,000 hooks. This declined to 0.07 fish per 1,000 hooks in 1978-80, a 36 percent CPUE decline. Thus, for a comparable time period the CPUE for the commercial fishery declined 36 percent for the southwest Pacific, and the CPUE for the recreational black marlin fishery declined 45 percent.

Striped Marlin

The 1969-76 catch of striped marlin per 1,000 hooks fished by the Japanese commercial longline fleet off the southern tip of the Baja California peninsula correlated positively with the CPUE of the recreational fleet as determined by the Survey (Fig. 7; Squire, 1982). Regression of the 1969-76 CPUE's for striped marlin attained by the Japanese longline fleet with that of recreationally caught striped marlin for the same period and in the same general area off Baja California Sur (5° areas, lat. 20°N by long. 105°W and lat. 20°N by long. 110°W) produced a reasonable correlation ($r = 0.81$). The CPUE of the Japanese longline fleet was much higher in the early and middle 1960's, before the start of the billfish angler survey in 1969, and it is reasonable to assume, based on historical data, that the angler CPUE was also higher. The limited amount of recreational fishery data available would support this.

Decline in the commercial longline catch rate of striped marlin off Baja California Sur appeared to be greater than that observed for recreational billfish anglers (Fig. 7). If CPUE rate is related to stock size, then the Survey could be measuring changes in stock size for a major area of fishing in the eastern Pacific. This is plausible because the area around the southern tip of Baja California Sur ac-

²Suzuki, Z., and M. Honma. 1977. Stock assessment of billfishes in the Pacific. Draft working paper, Billfish Stock Assessment Workshop, NMFS Honolulu Laboratory, Hawaii, 5-16 December 1974.

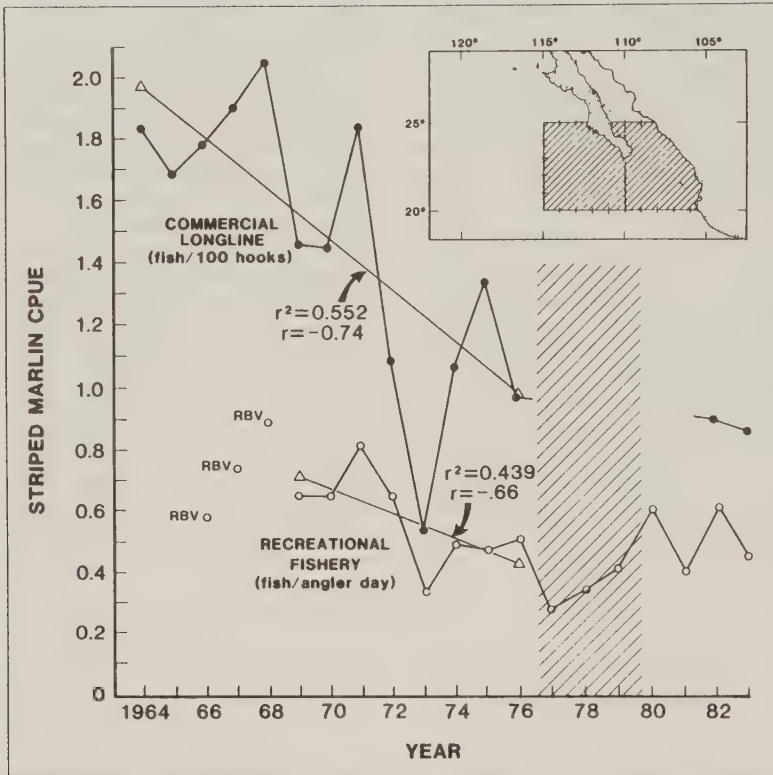


Figure 7.—Striped marlin CPUE and its regression for the commercial longline fleet 1964-76, two 5° long. by 5° lat. areas, and the Billfish Angler Survey for the southern portion of Baja California. The hatched area represents a period when longline operations were negligible within Mexico's 200-mile economic zone.

counts for about 25 percent of the commercial striped marlin catch in the eastern Pacific (east of long. 130°W). Downward CPUE trends in both sport and commercial fisheries indicate that the commercial longline fishing may have had an impact on the lower recreational billfish catch rates.

Longline fishing by foreign fishermen off Mexico for striped marlin, sailfish, and swordfish was interrupted in the spring of 1977 due to the enforcement of Mexico's 200-mile economic zone, which prohibited fishing by foreign fishermen except by permit from the government. In 1977 and 1978 no longline effort and catches of striped marlin were reported by the Japanese Fishery Agency

from around the tip of Baja California Sur, an area that produces some of the highest catch rates for striped marlin in the Pacific (Anonymous, 1956-80). As part of joint ventures between Mexico, Japan, Taiwan, and Korea, commercial longline fishing targeting on striped marlin, swordfish, and to a lesser extent on sailfish, was resumed in 1980. Effort and catch increased in 1981 and 1982. Longline catch data on the number of striped marlin per 1,000 hooks fished from portions of the joint venture longline operations about the southern tip of Baja California Sur are available for 1982 and 1983 (personal commun.). Striped marlin CPUE was calculated based on a 1982 catch of 13,489 fish using 1,494,610

hooks to give a CPUE of 9.03 fish per 1,000 hooks. The 1983 CPUE was 8.71 fish per 1,000 hooks fished based on a catch of 18,931 striped marlin using 2,104,716 hooks. The CPUE rate for 1982-83 is only slightly less than the CPUE rate the Japanese longliners experienced in 1976, before elimination of foreign longline fishing within Mexico's 200-mile economic zone.

The Billfish Angler Surveys in 1978, 1979, and 1980 show an increase in angler catch rate for Baja California Sur, reversing the downward trend of angler CPUE from 1969 to 1976 (Fig. 3, 7). The CPUE subsequently declined in 1983 to 1984.

The relaxation of commercial fishing effort in a local area (200 n.mi. zone) appears to have had a positive impact on billfish angler catch rates. Although recreational and commercial CPUE's noted in this paper and by Pristas (1980) appear to be positively correlated, the CPUE's may be following changes in local availability—that is, the fishing may not be noticeably affecting the total stock.

The economic value of recreational fishing for the large pelagics such as tunas and billfishes is substantial (Radonski, 1984; Herrick³). High catch rates of black marlin off Queensland, Australia, attract anglers from throughout the world, as does the high catch rates of billfish off Baja California Sur, Mexico. In some areas, such as about the tip of Baja California Sur, the recreational fishery is very important to the local economy.

It is important for fishery managers to know the economic value of the fishery and the level and trend of billfish angler catch rates as well. In southern California about 3,000 private boats are equipped with billfish fishing gear (Anonymous, 1979), yet the angler catch rate for striped marlin there is low—0.1 ± fish per day. Even at this low CPUE level, anticipation of a catch is great enough to warrant substantial expense and effort by

³Herrick, Samuel F., Jr. 1984. Socio-economic profile of the southern California billfish angler. NMFS Southwest Fish. Cent. Admin. Rep. LJ-84-12.

mostly local marine anglers. However, if the catch rates for striped marlin about the southern tip of Baja California Sur were to decline to such low levels (0.2-0.3 fish/angler day), foreign billfish anglers would be reluctant to undergo the expense and time to travel there and experience what would be rated as poor fishing for that area.

Summary

Data presented in this paper showing declines in commercial longline CPUE in relation to changes in angler CPUE for striped marlin off Baja California Sur and black marlin off Queensland suggest that recreational billfish fisheries are being affected by the commercial longline fisheries. The same was suggested by Pristas (1980) for billfish species in the Gulf of Mexico. When commercial longline fishing was curtailed within Mexico's 200 n.mi. economic zone in 1977-80, the recreational CPUE for striped marlin increased, which would be expected if the commercial fishery were having an effect.

However, in evaluating the relationship between the oceanic longline and localized, coastal recreational fisheries, it should be kept in mind that billfish are highly migratory and not likely to form local, vulnerable populations; the difference in total catch between most recreational and commercial fisheries is usually several orders of magnitude in favor of the commercial longline fishery; the magnitude of the effect of longline fishing on a localized recreational fishery

may only be accurately measured by angler catch rate in geographical areas where density and availability of a particular billfish stock are increased especially for the recreational fishery. In the eastern Pacific the mechanism by which the abundance of striped marlin is reflected in the localized recreational catch from off Baja California Sur may be high mobility of the fish throughout the eastern Pacific commercial fishing grounds coupled with increased availability when the fish nears the recreational fishing area.

Results from the Billfish Angler Survey indicate that management of pelagic billfish resources, where both commercial and recreational fisheries are participants, may require a determination of the minimum allowable angler catch rate based on socioeconomic analysis. This catch rate can be used as a bench mark when considering regulations that affect the interests of both the commercial and recreational fisheries.

Acknowledgments

The National Marine Fisheries Service wishes to express its appreciation to the many thousands of billfish anglers throughout the world who have responded to the annual survey. To Norman Bartoo, Earl Weber, Jean Michalski, and David Au in particular, goes my appreciation for review of the manuscript, and a special acknowledgment goes to Gerry Talbot for the initial development of the Pacific International Billfish Angler Survey.

Literature Cited

- Abramson, N. J. 1963. Distribution of angling effort in 1961. *Calif. Fish Game* 49:174-182.
- Anonymous. 1956-80. Annual report of effort and catch statistics by area on Japanese tuna longline fishery. Res. Dept. Fish. Agency Jpn., var. pagin.
- . 1979. Draft fishery management plan for billfish and sharks (eastern Pacific). Pac. Fish. Manage. Council, Portland, Oreg., Part I, Billfish, April 1979, 136 p.
- Calhoun, A. J. 1950. California angling catch records from postal card surveys: 1936-1948, with an evaluation of postal card nonresponse. *Calif. Fish Game* 36:177-234.
- Clark, J. R. 1960. The 1960 saltwater angling survey. U.S. Dept. Int., Fish Wildl. Serv., Bur. Sport Fish Wildl., Circ. 153, 36 p.
- Holland, K. 1985. Seasonality of catch per unit effort of the sport fishing fleet at Kewalo Basin, Hawaii. Univ. Hawaii, Sea Grant Tech. Rep. UNHH-SEAGRANT-TR-86-01, 10 p.
- Pristas, P. J. 1980. Big game fishing in the northern Gulf of Mexico during 1979. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., NMFS Tech. Memo. SEFC-23, 6 p.
- Radonski, G. C. (editor). 1984. Mid-Atlantic tuna and marlin fishing. *In* SFI Bull. 359 (Oct.), p. 4, 5.
- Squire, J. L. 1974. Angler catch rates for billfish in the Pacific Ocean. *In* R. S. Shomura and F. Williams (editors), Proc. Int. Billfish Symp., Kailua Kona, Hawaii, 9-12 Aug 1972, Part 2. Rev. Contrib. Pap., p. 290-295.
- U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.
- . 1982. 1982 Billfish newsletter U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish Cent., La Jolla, Calif. 12 p.
- Talbot, G. B., and P. G. Wares. 1975. Fishery for Pacific billfish of California and Mexico, 1903-69. *Trans. Am. Fish. Soc.* 104(1):1-12.
- Zurita Brito, H. 1980. Tendencia en la abundancia relativa del pez vela en la costa de Acapulco, Gro. Mexico. Memo. Dep. Pesca Delegacion Federal de Pesca en el Estado de Guerrero, 13 p.
- . 1985. Aspectos biológico-pesqueros del pez vela (*Isiophorus platypterus*) (Show y Nodder - 1791) en la Costa de Acapulco, Guerrero, Mexico. Univ. Autonomia de Guerrero, Thesis, 67 p.

Relation of Sea Surface Temperature Changes During the 1983 El Niño to the Geographical Distribution of Some Important Recreational Pelagic Species and Their Catch Temperature Parameters

JAMES L. SQUIRE

Introduction

In the coastal areas of the northeast Pacific, the distribution and apparent abundance of many species are affected more by environmental changes, as reflected in changes of sea surface temperature (SST), than by the catches in commercial and recreational fisheries. Natural fluctuations in marine populations resulting from changes in the physical and biological environment are known to significantly affect the determination of stock status and the level of catches (Sette, 1961; Ahlstrom, 1961, 1967; Anonymous, 1960; Uda, 1957, 1961; Miller, 1956; Jensen, 1930). Environmental changes such as small changes in SST either above or below the long-term mean significantly affect production by west coast pelagic fisheries. Continued periods of below normal temperatures in the late 1940's contributed to the decline of the Pacific sardine, *Sardinops sagax*, and are believed to have contributed to the abundance of the northern anchovy, *Engraulis mordax*, which was dominant from the mid-1950's to mid 1970's (Anonymous 1960; Sette, 1961, 1969).

The reasons for the extensive northward movement of marine fishes during abnormally warm periods are not well understood. However, these movements appear to be related to changes in the total environment (physical and biological) and reflect the requirements of the animals to sustain life. The interactions between the physical and biological environments are very complex, and the

effects of changes in most physical and biological characteristics on the behavior and distribution of marine fishes is little known. Sea surface temperature, one of the more easily measured physical environmental characteristics has been shown to have a positive correlation with the distribution of pelagic fish (Radovich, 1961; Hubbs, 1948).

Periods of unusually warm sea surface temperatures were reported along the northeast Pacific coast for 1859, 1926, 1931, 1941, 1957-58, 1972-73, 1976, and 1982-83. These periods, which are popularly called "El Niño" result from intense warming in the eastern tropical Pacific. This warming results from changes in the near-surface meteorology and oceanography, which in turn are related to a global shift in upper air pressure patterns. Previously, the most intense warm period after the record setting warm period of 1926 was in 1957-1958; however, the 1982-1983 warm period also appeared to be intense, exceeding that of 1957-1958 and possibly equaling that of 1926. The magnitude and duration of positive temperature anomalies observed off southern California during the warm periods of 1957-1958, 1972-1973, 1976-1977, and 1982-1983 are shown in Figure 1.

Warm periods appear to benefit the southern California fisheries for such subtropical species as the yellowtail, *Se-*

riola lalandei; Pacific barracuda, *Sphyræna argentea*; and Pacific bonito, *Sarda chiliensis*. The southern California recreational fishery also benefits from the northward migration of several other subtropical and tropical species, such as skipjack tuna, *Euthynnus pelamis*; yellowfin tuna, *Thunnus albacares*; and dolphin, *Coryphaena hippurus* (Radovich, 1960; Squire, 1983). Very warm temperatures may also have had a negative effect, as was evidenced during 1957-1958 and 1972-1973 by reductions of albacore, *Thunnus alalunga*, in the California recreational catch and of northern anchovy in the commercial and recreational bait fisheries. Off central California to Washington, catches during warm periods have been reduced in the troll fisheries for species of chinook salmon, *Oncorhynchus tshawytscha*; and coho salmon, *O. kisutch*.

Environmental changes, as reflected in SST changes, may be positive (above-normal SST's, or positive anomalies) or negative (below-normal water temperatures, or negative anomalies). The effects of prolonged high positive anomalies on the distribution of marine fishes off the west coast were well documented by Walford (1931), Radovich (1960, 1961, 1975), Ketchen (1956), Hubbs and Schultz (1929), Hubbs (1948), Bell and Pruter (1958), Royal and Tully (1961), and Fluharty (1984). Because of the impact of prolonged and strong positive temperature anomalies on the southern California catch of pelagic species having centers of distribution off Mexico, short-term intense warming periods have

James L. Squire is with the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

also been synonymous with better fishing—particularly off southern California and less so off central and northern California.

The period of above-normal SST's in 1982-83 resulted in some unusual migrations of tropical and subtropical fishes and invertebrates into northern latitudes more commonly occupied by subarctic species. An important factor in the northerly movement of species from tropical and subtropical areas is the timing and intensity of the higher temperatures (Fig. 1). Though temperatures increased, giving positive anomalies off southern California starting in July 1982, positive anomalies remained only about 2°F (1.1°C) above normal until December 1982, when this margin increased to about 4°F (2.2°C). The distribution and occurrence of species off southern California changed little during the period of slightly above-normal temperatures in summer and fall 1982, although Blesser (1984) noted an increase in catch of Pacific bonito. By January 1983, extensive effects on the changes in seasonality of billfishes off southern California were evident. Swordfish, *Xiphias gladius*, remained very abundant through January 1983 (an unusual condition), and good commercial catches were being made by drift gillnets when the season closed on 1 February, 1983. Striped marlin, *Tetrapturus audax*, were observed near Tanner Bank (west of San Clemente Island) in January 1983, although past catch records for southern California showed no catch of striped marlin in December or later. Early in 1983, red crabs, *Pleuroncodes planipes*, were abundant in the waters and on the beaches of southern California, indicating an increased development of the northeasterly coastal countercurrent (the Davidson Current), which in turn resulted in the northward movement of more-southerly forms of pelagic invertebrates. The strong countercurrent indicated that changing oceanographic conditions accompanied the positive temperature anomalies, resulting in more favorable conditions for the catch of tropical and subtropical pelagic species off southern California and northward.

The persistence of the 1983 warm period along the west coast is important.

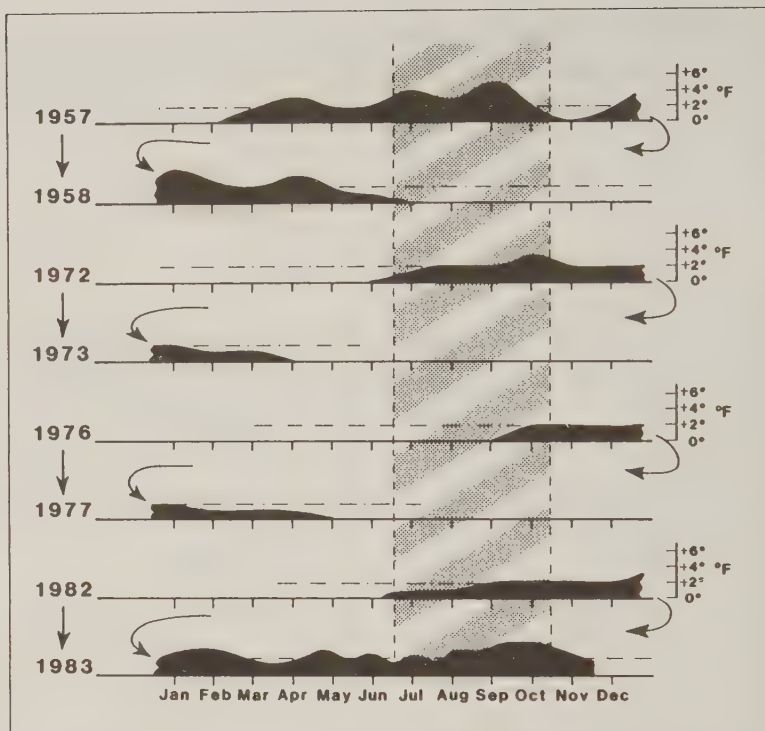


Figure 1.—Positive anomalies in SST's observed off southern California during the warm periods of 1957-58, 1972-73, 1976-77, and 1982-83. Striped area represents the major catch period off southern California, for yellowtail, Pacific barracuda, Pacific bonito, white seabass, chub mackerel, yellowfin tuna, and striped marlin.

Although positive temperature anomalies were not as high as in 1957, they lasted longer: 15 months (September 1982–November 1983) of positive anomalies 2°F (1.1°C) or more off southern California led to environmental changes that in turn resulted in significant changes in west coast recreational and commercial fisheries and in the geographical distribution of the fishery resources.

In 1983 several important southern California recreational and commercial species were reported much farther north than normal.¹ Most recent reports (Fluharty, 1984) give the following northernmost distributions in 1983.

Yellowtail, *Seriola lalandei*: Port Or-

ford, OR.

Pacific barracuda, *Sphyrna argentea*: Ketchikan, AK and Uyak Bay, Kodiak Isl. AK.

White seabass *Atractoscion nobilis*: Westport, WA.

Chub mackerel, *Scomber japonicus*: Oregon, Washington, into southern part of Puget Sound and north to Queen Charlotte Isl., B. C., Can.

Pacific bonito, *Sarda chiliensis*: Klawock, AK (Prince of Wales Isl.) (unverified rep. Kodiak Isl., AK).

Swordfish, *Xiphias gladius*: S. of Vancouver Isl., landed Flores Isl., B. C., Can.

Striped marlin, *Tetrapturus audax*: Off Monterey Bay and San Francisco area.

Yellowfin tuna, *Thunnus albacares*: Avila to Morro Bay, CA (reported from Monterey Bay, CA).

¹Fluharty, D., S. Crooke, and J. Fulton. Seattle, Wash. Personal commun.

Changes in coastal distribution of species common to southern California into the northern latitudes in past have been well documented. Miller and Lea (1972) recorded the northern distributional limits of important pelagic species common to southern California and Baja California, Mexico, as:

Yellowtail	S. Washington
Pacific barracuda	Kodiak Isl., AK
White seabass	Juneau, AK
Chub mackerel	Gulf of Alaska
Pacific bonito	Gulf of Alaska
Striped marlin	Oregon
Swordfish	Oregon
Yellowfin tuna	Pt. Buchon, CA

The northern distribution limits observed for these fishes in 1983 are not substantially different from past records, although yellowfin tuna and swordfish may have established northern coastal distribution records in 1983. Southern distribution records are sometimes set for northern species during warm periods; Phillips (1958) described such southerly extensions for three species caught off California in 1957.

Most literature on the effects of the warm period on fish catch involves descriptions of the geographical extent of distribution. Some west coast researchers have reviewed the catch of fish off California in relation to variable sea surface temperature, and others the effects of temperature changes in northern waters to catch (Radovich, 1960, 1961; Hubbs, 1948; Ketchen, 1956; Bell and Pruter, 1958.) Here I present information on mean sea surface temperatures at the point of capture ("catch temperatures") that have been observed for several species common to southern California recreational fisheries, and on the geographical extension of these optimal catch temperatures into the northern latitudes off the west coast during the 1983 period of intense warming.

Materials and Methods

In 1963 monthly studies of coastal sea surface temperatures by airborne infrared surveys were started by the Tiburon Marine Laboratory (now the Tiburon Laboratory of the National Marine Fisheries Service, Southwest Fisheries Cen-

ter) in cooperation with the U.S. Coast Guard. The studies were done to obtain fine-scale SST data for use in relating surface temperatures to fish catch. The results of these temperature surveys, and a special series of surveys off San Diego, Calif., which were done for studies on the relation of temperature to the catch of pelagic species, were published by Squire (1971, 1978). The mean catch temperature, temperature ranges, and standard deviation from the mean by month for a number of species for various areas (10' long. $\times$ 10' lat.) off central and southern California were determined by Squire (1982). Figure 2 illustrates these temperature and catch distributions (for yellowtail). Chinook and coho salmon data were reviewed for central California, and yellowtail, Pacific barracuda, white seabass, Pacific bonito, and chub mackerel data were reviewed for southern California. Data for these studies were collected during a period of nearly normal SST in 1963-1968.

The latitudinal increase in SST during periods of warming results in a displacement northward of mean catch temperature parameters and may indicate the possible extent of a parallel northward displacement of these species. From published catch-temperature data (Squire, 1982) and unpublished observations, I developed data on mean catch temperatures for several pelagic species off southern California, for salmon off central California, and for two oceanic pelagic species (striped marlin and yellowfin tuna) that are frequently caught off southern California in summer. I have also compiled the monthly mean ($\bar{x}$ ct) and standard deviation about the mean ($\bar{x}$); high mean ($H\bar{x}$ ct), and low mean ($L\bar{x}$ ct) catch temperatures and the range of temperatures at which these species were observed (Table 1). I examined SST charts produced semimonthly during 1983 by the Inter-American Tropical Tuna Commission and the National Weather Service and noted the geographical extent of mean catch temperatures for each time period. Throughout the area south of the most northward geographical extension of the low mean catch temperatures (Fig. 3-7 and 9), all sea surface temperatures equaled or exceeded the low mean catch temperature.

Results

Observations of the changes in mean catch temperatures in relation to SST changes off the U.S. west coast are reviewed separately here for various coastal pelagic species.

Yellowtail

The pelagic coastal migratory yellowtail commonly ranges from the southern tip of Baja California, Mex. to near Point Conception, Calif. It is one of the most important recreational fishes in southern California and an important recreational and commercial species in Mexico. The major sport fishing areas at the northern end of the range are the Coronado Islands, Mex., and kelp beds off San Diego and Catalina Island, Calif. Yellowtail are caught off southern California in large numbers only during their summer northward migration from Baja California and are rarely caught north of Point Conception except during years of anomalous warm SST's.

The mean catch temperature for yellowtail caught off southern California was 63.2°F (17.3°C) with a standard deviation of $\pm 3.6^\circ\text{F}$ (2.0°C). The low mean catch temperature of 57°F (13.9°C) was recorded during March and the high mean catch temperature of 70.0°F (21.1°C) during August; the total catch in March was only 2 percent of that in August. The range of temperatures at which yellowtail were observed to be caught off southern California was 51.0°-74.0°F (10.6°-23.3°C).

The shift of the warmer SST environment northward during summer 1983 was presumably responsible for the taking of yellowtail north of Point Conception; catches were also reported as far north as Port Orford, Oreg., in August 1983. Figure 3 illustrates for semi-monthly periods from 16 April to 30 November, 1983, the movement of the geographical position to mean catch temperature, the latitudinal extent of SST's within one standard deviation, and the monthly low and high mean catch temperatures.

The southern California mean catch temperature of 63.7°F (17.3°C) was at about lat. 28°N in late April through May (Fig. 3); at the latitude of southern Cali-

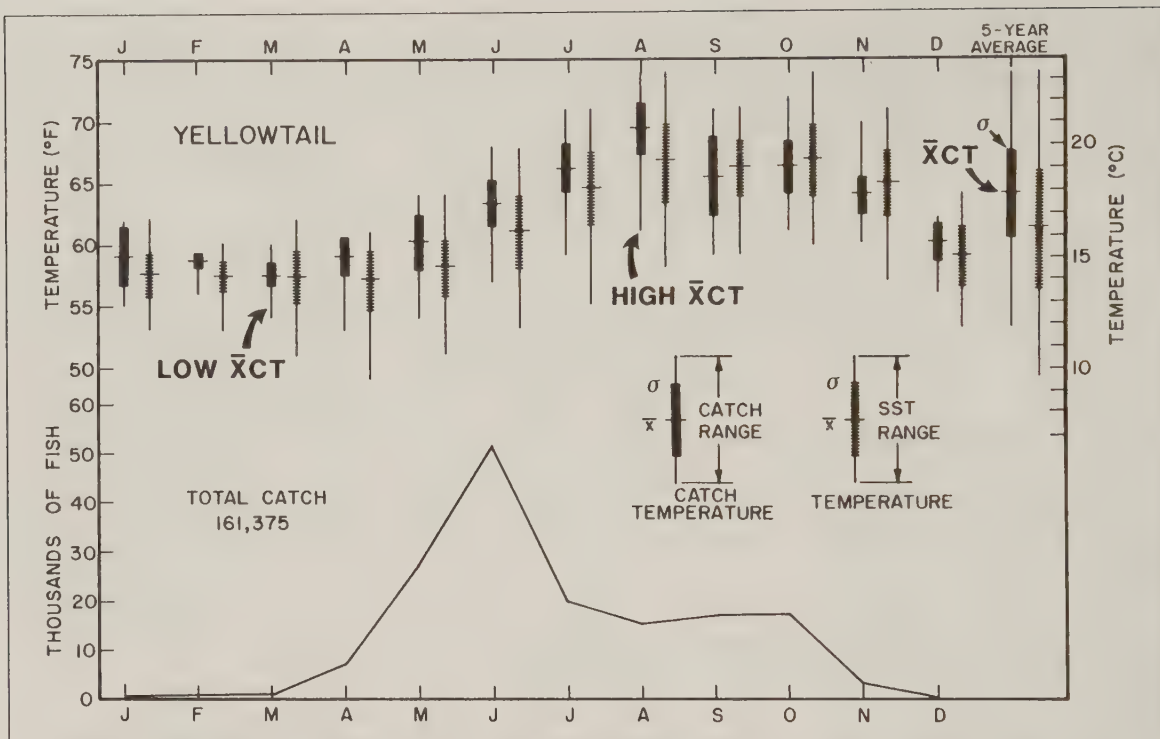


Figure 2.—Distribution of yellowtail catch off southern California and northern Mexico by month, August 1963-July 1968 for total catch, catch temperature, and SST range and means, and the standard deviations about the means (from Squire, 1982).

Table 1.—Mean catch temperatures and temperature ranges for salmon caught off northern California and for other species caught off southern California.

Species	Mean catch temperature observed									
	High $\bar{x}$ ($\bar{x}_{Hct}$) ¹		Low $\bar{x}$ ($\bar{x}_{Lct}$) ²		Overall $\bar{x}$ ($\bar{x}_{ct}$) ³		SD.		Temperature range	
	°F	°C	°F	°C	°F	°C	°F	°C	°F	°C
Yellowtail	70.0	21.1	57.0	13.9	63.2	17.3	3.6	2.0	51.0-74.0	10.6-23.3
Pacific barracuda	69.0	20.5	57.8	14.3	64.4	18.0	4.6	2.8	51.0-74.0	10.6-23.3
Pacific bonito	67.0	19.4	54.0	12.2	64.8	18.2	3.6	2.0	51.0-73.0	10.6-22.8
White seabass	67.0	19.4	56.8	13.8	65.2	18.4	4.5	2.4	52.5-75.0	11.4-23.8
Chub mackerel	68.0	20.0	57.0	13.9	64.0	17.8	4.0	2.2	50.0-73.5	10.0-23.0
Salmon	58.5	14.7	52.0	11.1	56.8	13.8	3.2	1.8	45.5-62.5	7.5-16.9

¹ $\bar{x}_{Hct}$ - highest monthly mean temperature.

² $\bar{x}_{Lct}$ - lowest monthly mean temperature.

³ $\bar{x}_{ct}$ - overall mean catch temperature.

fornia from late June through July; and slightly north of the latitude of Point Conception from August through mid-September. The low mean catch temperature observed for yellowtail off southern California reached latitudes north of 50°N during only one period—1-15 Au-

gust during the period when a specimen was reported at Port Orford, Oreg. Sea surface temperatures cooled slightly in the northern latitudes in late August, but when they warmed again in early September the geographical position of the southern California mean catch tempera-

ture was displaced further north by late September to the approximate latitude of Monterey, Calif. (lat. 37°N). Sea surface temperatures declined in early October southward, to a point where the geographical point of the mean catch temperature was below Point Conception by early November. In 1983 yellowtail were reported off central California and SST's were high enough to extend the low mean catch temperature northward to lat. 50°N, making it reasonable to assume from temperature data that yellowtail may have migrated farther northward than recorded.

Pacific Barracuda

High catch areas in southern California are normally along the coast off San Diego, near San Clemente, and off Huntington Beach; peak catches are usually recorded in September. A few barracuda

are taken off Santa Barbara and the Channel Islands from August to October. Pacific barracuda are not common north of Point Conception.

The mean catch temperature for Pacific barracuda caught off southern California was 64.4°F (18.0°C) with a standard deviation of $\pm 4.6^\circ\text{F}$ ($\pm 2.8^\circ\text{C}$). The SST range at which Pacific barracuda were caught off southern California was 51.0°–74.0°F (10.6°–23.3°C). The monthly mean catch temperature was lowest in February at 57.0°F (13.9°C) and highest in August at 69°F (20.6°C). The catch in February was only 12.5 percent of that in August.

In summer 1983 in the more northern latitudes ($> \text{lat. } 35^\circ\text{N}$), increased SST was associated with a northward movement of Pacific barracuda. The low mean catch temperature of 57.0°F (13.9°C) extended well north of Point Conception (the normal northern ecological boundary for the species) in early June 1983, and above lat. 50°N in early August and September (Fig. 4). The mean catch temperature of 64.4°F (18.0°C) was present slightly north of Point Conception in early August through mid-September, and was further north, off Monterey Bay, in late September. By early November it moved progressively southward to a point south of Point Conception. From July through mid-September temperatures favorable to Pacific barracuda were common along the California, Oregon, and Washington coasts and suitable temperatures for more northward migration appeared to be present in early August through mid-September. Catches were reported off Oregon, Washington, and as far north as Ketchikan, Alaska, (28 August, 1983) and at Uyak Bay, Kodiak Island, Alaska (August 1983).

Pacific Bonito

The Pacific bonito migrates considerable distances along the coast of Baja California, Mex., and into southern and central California. As with the Pacific barracuda, northern latitudinal distribution expands greatly during periods of anomalous warm-water conditions in the northeast Pacific (Radovich, 1961). Catches off southern California usually peak in August.

The distribution of the Pacific bonito is

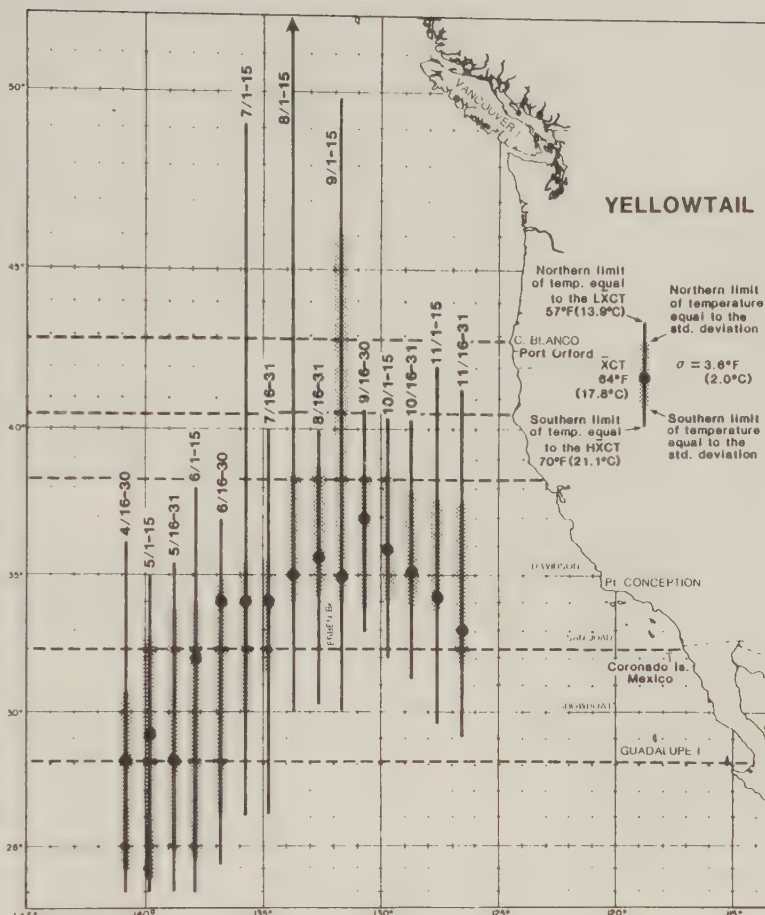


Figure 3.—Latitudinal extent semimonthly periods in 1983 of the high mean catch temperature (HXCT) and low mean catch temperature (LXCT), shown by vertical bars, and mean catch temperature (XCT; solid circles) $\pm$ one standard deviation (irregular lines above and below the means) for yellowtail caught off southern California.

usually considered to be centered off Baja California, Mex. It was uncommon off southern California from the late 1930's until the warm year of 1957. It moved northward during the warm years of 1957–58. After declines in the population of Pacific sardine, chub mackerel, and jack mackerel, *Trachurus symmetricus*, in the early 1960's, the southern California purse seine fleet increased its fishing effort on the Pacific bonito. Apparent abundance levels decreased sub-

stantially in the late 1960's until the warm period of 1972, when northward movement of Pacific bonito from the south again resulted in an increase in apparent abundance and commercial catch off southern California (Squire, 1983). The Pacific bonito resource then decreased in the mid-1970's to lower levels of abundance and catch, as it did in the late-1960's.

Mean catch temperature for Pacific bonito off southern California was

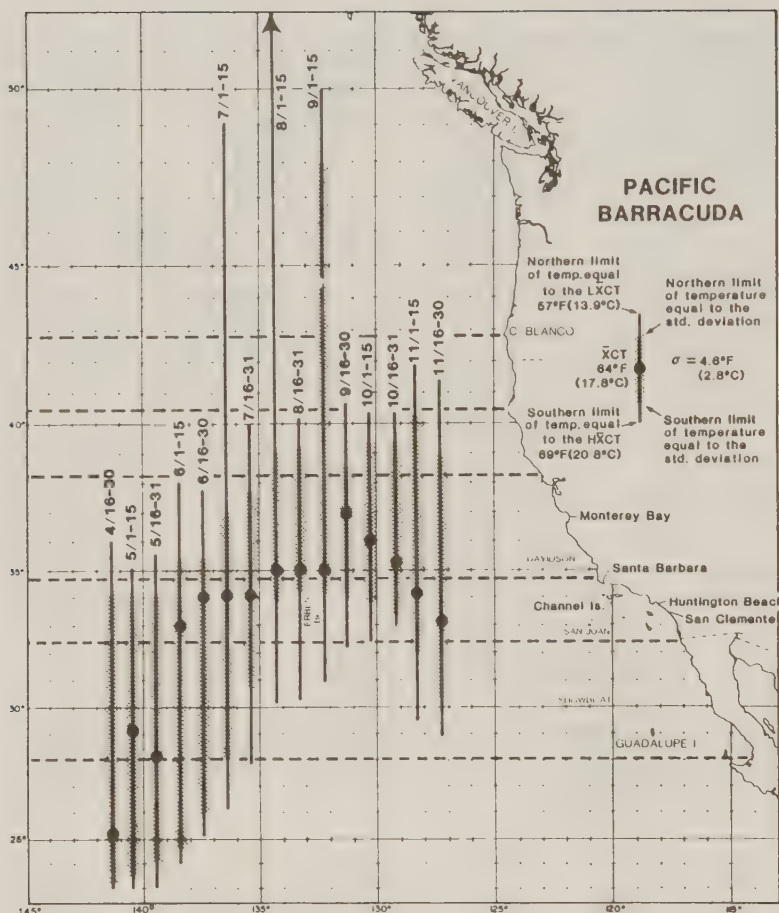


Figure 4.—Latitudinal extent by semimonthly periods in 1983 of the high mean catch temperature (H_{TCT}) and low mean catch temperature (L_{TCT}), shown by vertical bars, and mean catch temperature ($\bar{x}_{TCT}$; solid circles) $\pm$ one standard deviation (irregular lines above and below the means) for Pacific barracuda caught off southern California.

64.8°F (18.2°C) with a standard deviation of $\pm 3.6^\circ\text{F}$ ($\pm 2.0^\circ\text{C}$), and SST's at which Pacific bonito were caught ranged from 51.0° to 73.0°F (10.6°–22.8°C). The mean catch temperature was observed to be lowest in February at 54.0°F (12.2°C) and highest in August at 67.0°F (19.4°C); catches during February were only 5.6 percent of those during August.

Pacific bonito appear to be highly responsive to warming in the northern latitudes and are frequently caught off the

coasts of northern California, Oregon, and Washington, and into the Gulf of Alaska during warm years. As shown by the geographical locations of mean catch temperatures as observed from 15 April through 30 November, 1983 (Fig. 5), the shift toward more northern latitudes of the low and mean catch temperatures observed off southern California suggests more optimum conditions for northward migration of Pacific bonito than for yellowtail or Pacific barracuda. Mean catch

temperatures were south of southern California until July, off southern California until mid-August, and then moved north of Point Conception. The low mean catch temperature extended into latitudes above 52°N for most of the period from July through mid-September, indicating favorable temperatures for the species in the areas off Canada and into the Gulf of Alaska. Pacific bonito were reported caught during the summer off Kalawock and Kodiak Island, Alaska.

White Seabass

Major catch areas for white seabass along the southern California coast are from San Diego to Dana Point, with the greatest numbers being caught near Oceanside. The catch peaks in August.

White seabass have been caught in Monterey Bay and off San Francisco during warm-water years (Frey, 1971) and off Juneau, Alaska (Miller and Lea, 1972). A population of white seabass is also reported in the northern portion of the Gulf of California; however, the center of distribution for the Pacific population is considered to be between Point Conception, Calif., and Ballenas Bay, Baja California Sur, Mexico. Both recreational and commercial catches have declined substantially since the 1950's, and the recreational fishery catch off southern California declined to very low levels after the late 1950's (Young, 1969).

The mean catch temperature observed off southern California for white seabass was 65.2°F (18.4°C) with a standard deviation of $\pm 4.5^\circ\text{F}$ ($\pm 2.4^\circ\text{C}$) and ranged in southern California from 52.5° to 75.0°F (11.4°–23.8°C). The mean catch temperature was highest in August at 67.0°F (19.4°C), and lowest in April at 56.0°F (13.3°C). Catches during April were 16.6 percent of those during August.

Geographically, the mean catch temperature for southern California in 1983 was near the latitude of Cedros island in late April through May (Fig. 6), had moved northward to off southern California in early July, and reached a point north of Point Conception in late August through October. The low mean catch temperature for southern California was north of lat. 52°N from late July through mid-September. White seabass were

recorded off Westport, Wash., during mid-July 1983.

Chub Mackerel

Abundance of chub mackerel was low in the early 1960's. Beginning in 1976, a series of good year classes made this species one of the more important commercial and recreational species in southern California by 1980. Recreational fishing areas produce substantial catches of chub mackerel off San Diego, Dana Point, and Santa Monica Bay, and near Catalina Island. Catches were low during November-May, and peaked in August.

Mean catch temperature for chub mackerel off southern California was 64.0°F (17.8°C) with a standard deviation of $\pm 4.0^\circ\text{F}$ ($\pm 2.2^\circ\text{C}$), and SST's observed where Pacific mackerel were caught off southern California ranged from 50.0° to 73.5°F (10.0°-23.0°C). The monthly mean catch temperature was highest at 68.0°F (20.0°C) in August, and lowest in February at 57.0°F (13.9°C). The catch during February was 20.0 percent of that observed in August.

The mean catch temperature observed for chub mackerel off southern California shifted from the waters off Baja California, Mex., in April and May to waters off southern California by early June (Fig. 7), to a point north of the latitude of Point Conception by early August, and a point near lat. 32°N (Monterey and San Francisco) by late September. The point of mean catch temperature remained north of Point Conception until late October. The low mean catch temperature was above lat. 50°N during the period 1-15 August, 1983. Pacific mackerel were reported caught off the northern California, Oregon, and Washington coasts; into the southern part of Puget Sound, Wash.; and north to the Queen Charlotte Islands, B.C., Can., during the period June-September 1983.

Yellowfin Tuna

One of the most unusual occurrences off southern California of a tropical species infrequently caught there was reflected in the large catch of yellowfin tuna in the recreational fishery in 1983. Historical catch data for recreational fishing in southern California indicated that warm periods, such as those of 1957 and

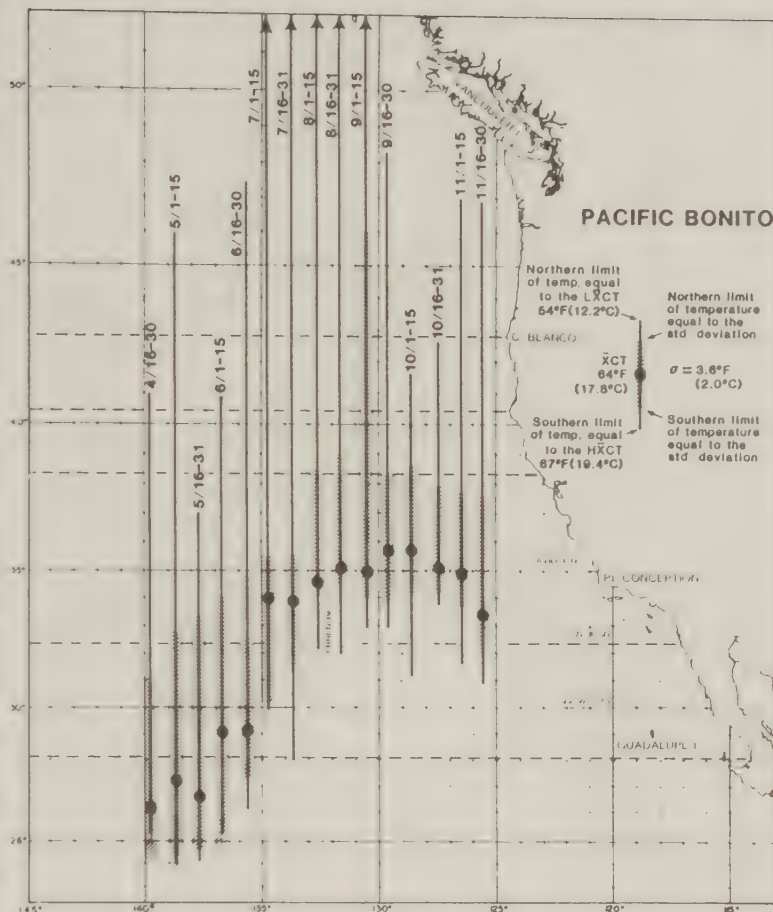


Figure 5.—Latitudinal extent by semimonthly periods in 1983 of the high mean catch temperature (Hxct) and low mean catch temperature (Lxct), shown by vertical bars, and mean catch temperature (xct; solid circles) $\pm$ one standard deviation (irregular lines above and below the means) for Pacific bonito caught off southern California.

1972, produced substantial increases in catches of skipjack tuna and dolphins. However, yellowfin tuna catches increased only slightly in 1957-58 (Squire, 1983). Recreational catches recorded by Young (1969) were nil in 1953 and 1954, 1 fish in 1955, 78 in 1956, 325 in 1957 (the warm year), 13 in 1958, and 4 in 1959. During this 7-year period, the number of angler days ranged from 502,000 to 557,000, indicating that angler effort did not change markedly during the period. In April 1983, Squire

(1983) forecast the possible effects of the 1982-83 warm period on southern California recreational fishing if the El Niño continued through 1983. Although the forecast (based on historical catch data) did not mention substantial increases in recreational catches of yellowfin tuna, the 1983 recreational catch of yellowfin tuna off southern California clearly set a record: More than 89,000 yellowfin tuna were reported caught by the San Diego commercial sportfishing boat fleet alone during the year (Anonymous, 1984).

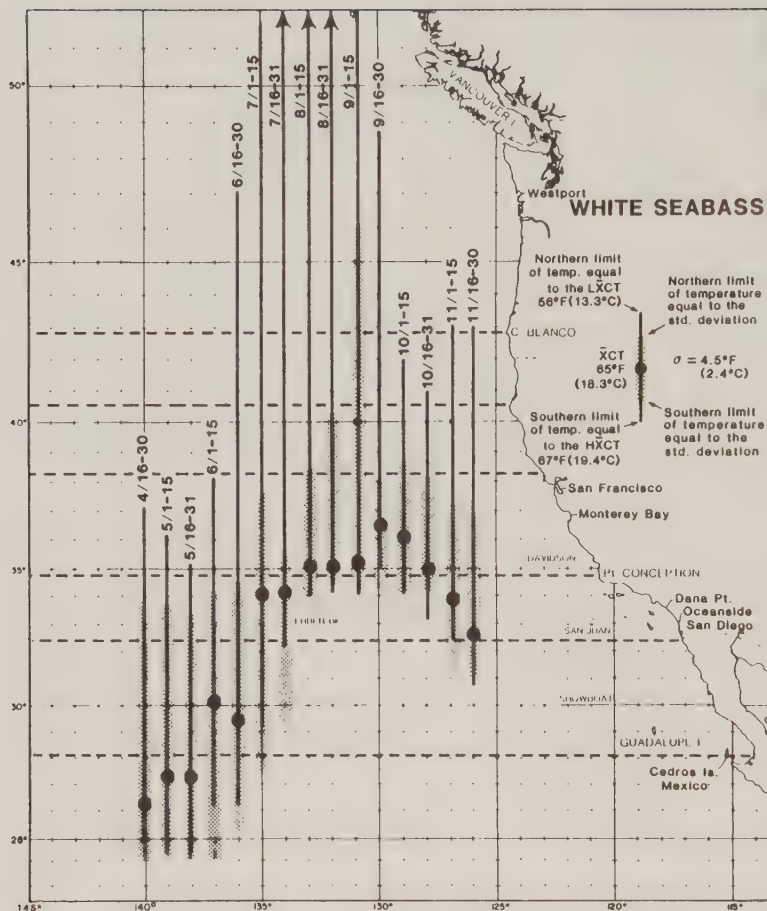


Figure 6.—Latitudinal extent by semimonthly periods in 1983 of the high mean catch temperature (Hxct) and low mean catch temperature (Lxct), shown by vertical bars, and mean catch temperature ($\bar{x}$ ct; solid circles) $\pm$ one standard deviation (irregular lines above and below the means) for white seabass caught off southern California.

Catches from the commercial sportfishing boats in other southern California ports were substantial, and catches by private boats will further increase the record 1983 total. Skipjack tuna were also caught in large numbers—San Diego landings alone totaled 73,000 fish and about 3,400 bigeye tuna, *Thunnus obesus*, were landed (Anonymous, 1984).

Inasmuch as the catches of yellowfin tuna are relatively uncommon off southern California, catch temperature data for

the species in the region are not available. The most northerly area where yellowfin tuna are ordinarily taken in substantial quantities with commercial purse seines extends from west of Cabo San Lucas to south of Cedros Island, Baja Calif., Mex. The seine fishery is common in the area west of Cabo San Lucas in April, May, and June, and shifts northward to the area south of Cedros Island in August to October. Since high mean and low mean catch temperatures for this species in the area of interest are not known,

Table 2.—Monthly mean sea surface temperatures for two yellowfin tuna fishing areas off the west coast of Baja California, Mex.

Month	Mean SST's in °F and (°C)	
	West of Cabo San Lucas	South of Cedros Island
April	70°F (21.1°C) ¹	62°F (16.7°C)
May	70°F (21.1°C)	63°F (17.2°C)
June	72°F (22.2°C)	63°F (17.2°C)
July	79°F (26.1°C)	68°F (20.0°C)
August	82°F (27.8°C)	70°F (21.1°C)
September	83°F (28.3°C)	72°F (22.2°C)
October	82°F (27.8°C)	71°F (21.7°C)
November	80°F (26.7°C)	68°F (20.0°C)
December	74°F (23.3°C)	67°F (19.4°C)

¹Underlining indicates average temperature for the month and area having major catches of yellowfin tuna.

I must rely on the determination of average SST by examination of monthly average SST charts (Anonymous, 1969). These charts indicate the mean SST's by month for the area west of Cabo San Lucas and to the south of Cedros Island; temperatures observed are given in Table 2.

The mean temperature during periods of high catches in the area west of Cabo San Lucas was 70.7°F (21.5°C) and 71.0°F (21.7°C) south of Cedros Island. These data indicate that 71°F (21.7°C) could be considered as an optimum catch temperature. Use of this value indicates that the optimum temperatures for yellowfin tuna were located south of Cedros Island through July 1983 (Fig. 8) Sea surface temperatures increased north of Cedros Island in August, and temperatures approximating the optimum catch temperature were common off southern California in early August through October 1983. The major area of yellowfin tuna fishing by the recreational fishing fleet off southern California extended from northern Baja California, Mex., north to the latitude of Los Angeles.

Striped Marlin

Striped marlin are caught by recreational anglers with rod and reel and sometimes by commercial drift gillnets and harpoons off southern California during late summer and early fall. Striped marlin are common all year in Pacific waters off the west coast of Baja California Sur, Mex. (south of lat. 27°N). The eastern Pacific distribution was described by Miller and Lea (1972) as from Chile to Oregon.

Catch temperature studies off southern California reported by Squire (1974) indicated that the mean temperature at which striped marlin are caught off southern California is 67.8°F (19.9°C) with the standard deviation of $\pm 0.5^\circ\text{F}$ ($\pm 0.25^\circ\text{C}$). Striped marlin are caught off southern California at a temperature range of about 61°-73°F (16.1°-22.8°C). Catches appear to increase at an exponential, but highly variable, rate relative to increases in temperatures (Squire, 1985).

For the period 1 June through 30 November, 1983, the geographical locations of the mean catch temperature and the approximate normal temperature range are shown in Figure 9. Mean catch temperatures were present south of southern California in June and July. Sea surface temperatures increased off southern California in early August, and the mean catch temperature value was observed to be common to these waters from August through October. The low mean catch temperature extended northward to off San Francisco from early September to mid-October. Striped marlin were caught off the San Francisco area by drift gillnets and one was reported caught in Monterey Bay by rod and reel.

Pacific Salmon: Central California

Sea surface temperatures observed for the major recreational fishing areas for Pacific salmon from Monterey Bay to Bodega Bay, Calif., normally range from about 45° to 63°F (7.2°-17.2°C). Water temperatures in this area are low during January through May or June and lowest about April. Temperatures increase slightly from June through September, when the mean temperature peaks, and then usually begins to drop in October.

Peaks in the salmon catch for the fishing area off San Francisco (the major catch area) occur in March and July. To the north, off Bodega Bay, the catches peak in July and August. To the south, off Monterey, two catch peaks occur—one in May and one in July. Chinook salmon are most often caught, because spawning chinook salmon are in the Sacramento River system during most of the year, and these fish pass through the

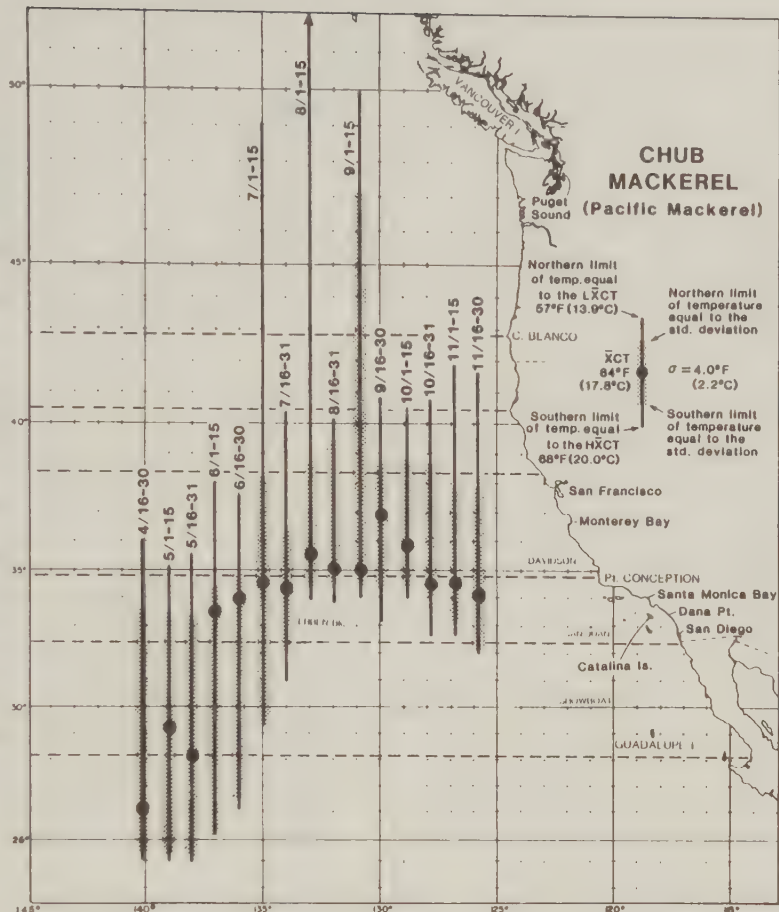


Figure 7.—Latitudinal extent by semimonthly periods in 1983 of the high mean catch temperature ($\bar{H}ct$) and low mean catch temperature ($\bar{L}ct$), shown by vertical bars, and mean catch temperature ($\bar{x}ct$; solid circles) $\pm$ one standard deviation (irregular lines above and below the means) for chub mackerel caught off southern California.

major ocean fishing areas off central California. The fall run of chinook salmon is the largest, and fish aggregate off the San Francisco Bay area before the spawning migration.

Salmon catches off central California in 1983 followed past trends toward lower catches during abnormally warm periods. Before the 1957 warm period, the recreational catch off California (Young, 1969) had increased from about 80,000 to 90,000 fish in 1952 and 1953 to 114,000 fish in 1956. During the

warm-water year of 1957, catches dropped to about 45,000 fish and remained at this lower level of 40,000-50,000 fish for several years.

About 50 percent of the salmon catch in the area from Monterey Bay to Bodega Bay is made at water temperatures of 51.8°-56.0°F (11.0°-13.3°C). The mean catch temperatures during the months of highest production ranged from 52.6° to 53.8°F (11.4°-12.1°C), off Monterey in May and June; off San Francisco the best months were June and July at 52.8°-

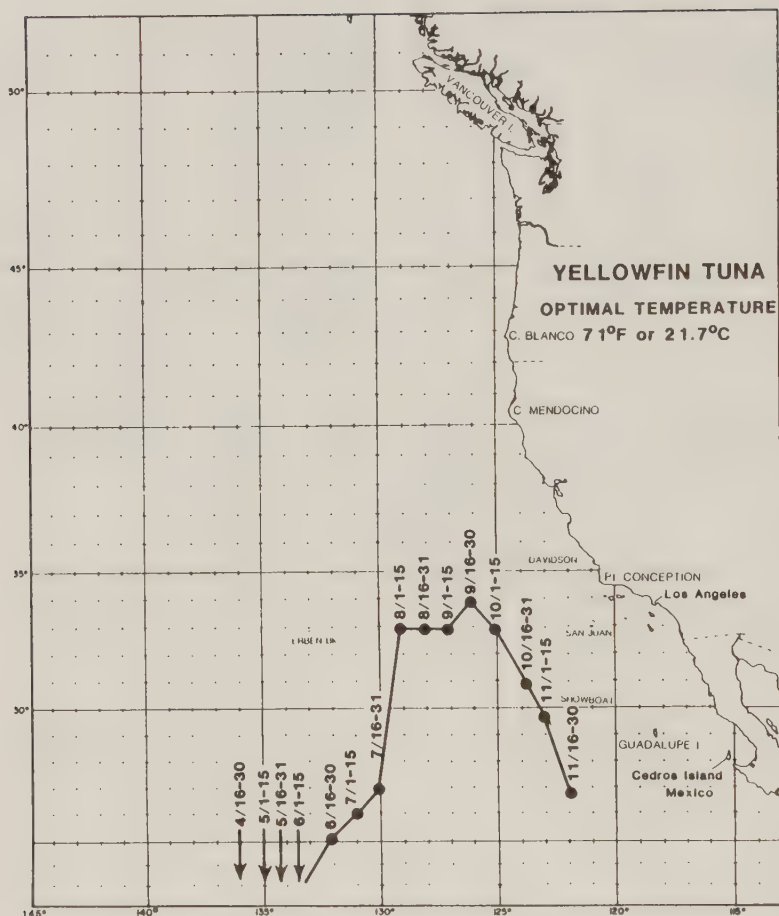


Figure 8.—The semimonthly latitudinal location of optimal catch as observed off Baja California, Mex. (71°F or 21.7°C), for yellowfin tuna during the 1983 fishing season.

54.4°F (11.6°-12.4°C), and off Bodega Bay the best catches were in July and August with a range of 51.6°-52.4°F (10.9°-11.3°C). Using temperatures of 53°F (11.7°C) for the Monterey and San Francisco areas, and 52°F (11.1°C) for off Bodega Bay as values representing optimal catch temperatures, a comparison of these temperatures with those obtained from 15-day coastal SST charts for the period 1 January through 30 October, 1983, shows that all temperature values were found to be above the optimal values observed during normally high catch periods (Table 3).

Discussion and Summary

Analysis of catch temperatures (Squire, 1982) shows that the deviation of catch about the mean catch temperature is considerable. Therefore, the mean catch temperature (high $\bar{x}$, low $\bar{x}$, or $\bar{x}$) must be viewed as it is statistically—a measure of the location of central tendency. The superficial aspects of sea surface temperature in relation to catch should be taken into consideration when one evaluates the semimonthly geographical location of the high and low mean and mean catch temperature given for

yellowtail, Pacific barracuda, Pacific bonito, white seabass, and chub mackerel in Figures 3-7, and optimum catch temperatures for yellowfin tuna and striped marlin in Figures 8-9 and salmon in Table 2.

Although fishes and invertebrates are poikilothermic and function over a rather wide range of temperatures (Brett, 1956), they tend to concentrate in environments that are favorable to their metabolic requirements for successful development (Uda, 1961). Subtropical species of yellowtail, Pacific barracuda, Pacific bonito, white seabass, and chub mackerel common to southern California waters have been observed to be caught off southern California at SST's of 50.0°-75.0°F (10.0°-23.9°C), with these species showing a temperature range of from 20°F (11.1°C) to 23.5°F (13.0°C). Observations of SST's in the northeast Pacific during summer and early fall in 1983 would indicate the minimum temperatures at which some of these subtropical pelagic species caught off southern California were commonly observed in the northern portion of the Gulf of Alaska. The degree of environmental change, as exemplified by SST increases in the northern latitudes, results from physical changes in the California Current system (Reid et al., 1958), such as increases in the magnitude of the northward flowing subtropical countercurrent (the Davidson Current) and a reduction in coastal upwelling. These physical changes result in warming of the upper layers of the ocean, enabling such species as chub mackerel and white seabass to migrate to the coasts of Oregon, Washington, British Columbia, and (for some species as Pacific barracuda and Pacific bonito) even further north into the Gulf of Alaska.

The population sizes of coastal pelagic species of Pacific barracuda, white seabass, and yellowtail were considerably smaller in 1982-83 than during the warm period of 1957-58 (MacCall et al.²), whereas the populations of Pacific bonito and chub mackerel were only moderately reduced. Consequently the probability of

²MacCall, A. D., G. Stauffer, and J. P. Troadec. 1974. Stock assessments for southern California recreational and commercial marine fisheries. NMFS Southwest Fish. Cent. Admin. Rep. LJ-74-24, 144 p.

recovering Pacific bonito and chub mackerel was higher than that of recovering specimens of the other three species.

Along the coast from about Cedros Island, Baja California, to near Cape Blanco, Oreg., during the summers of normal years, a series of SST changes appear to be related to the northward coastal migration of many subtropical and tropical species (Hubbs, 1948). The southern upwelling area (Fig. 10) extends from north of Cedros Island (lat. 28°N) to about southern California (lat. 32°N). South of this area, SST's are generally higher. Increases in temperature during warm years have resulted in exponential increases in catches of striped marlin off southern California. Catches of Pacific bonito, dolphin, skipjack tuna, and yellowtail increase off southern California when upwelling is reduced in the area south of southern California.

Because the southern California Bight (area near U.S.-Mexico border to Point Conception) is characterized by a counterclockwise current flow, SST's in the northern portion (between long 119° and 120°W) are only slightly lower than those in the southern portion (Gulf of Catalina). Fish migrating into the Southern California Bight from the south encounter few environmental temperature barriers until they reach the Point Conception area (lat. 34°30'N). Point Conception is at the southern end of the major upwelling area that extends north to about Cape Blanco, Oreg. (Fig. 10), and is recognized as an ecological barrier to the northward migration of subtropical fishes (Hubbs, 1948). The upwelling

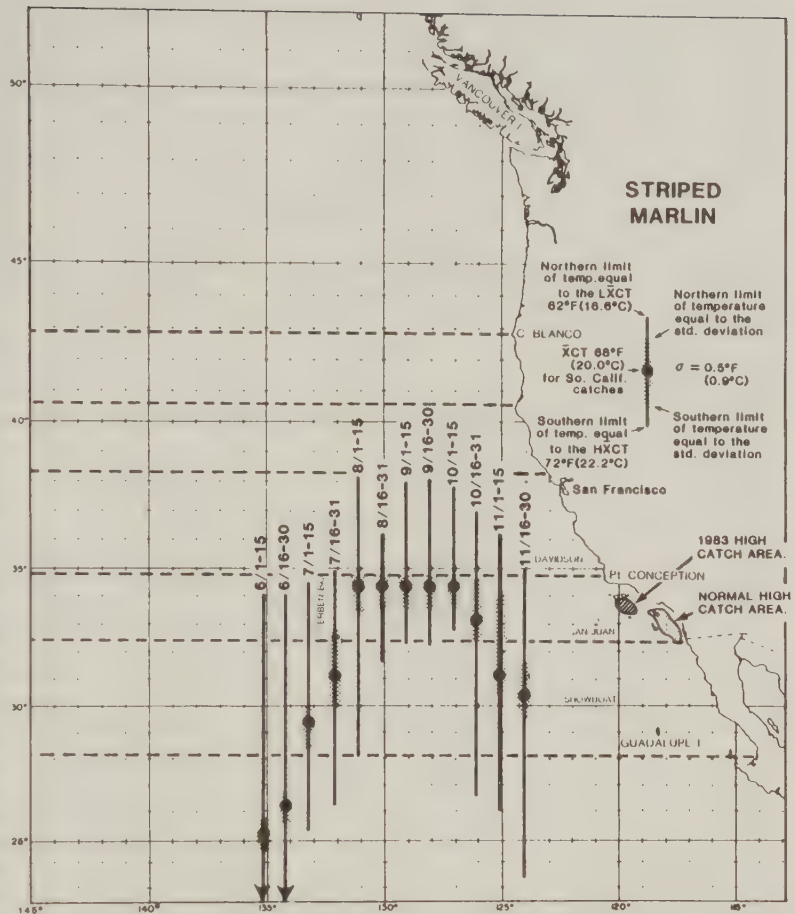


Figure 9.—Latitudinal extent by semimonthly periods in 1983 of the high mean catch temperature (Hxct) and low mean catch temperature (Lxct), shown by vertical bars, and mean catch temperature (xct; solid circles) $\pm$ one standard deviation (irregular lines above and below means) for striped marlin caught off southern California.

Table 3.—Upward (positive) deviation of sea surface temperatures observed in 1983 off Monterey Bay, San Francisco, and Bodega Bay in relation to optimal catch temperature values.

Locality and optimal catch temperature	January		February		March		April		May		June		July		August		September		October	
	1-15	16-31	1-15	16-29	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-30	1-15	16-31	1-15	16-31	1-15	16-30	1-15	16-31
Monterey Bay 53°F (11.7°C)	6	6	5	5	3	4	4	2	4	2	6	6	6	6	10	9	16	10	11	10
	3.3	3.3	2.8	2.8	1.7	2.2	2.2	1.1	2.2	1.1	3.3	3.3	3.3	3.3	5.6	5.0	3.3	5.6	6.1	5.6
San Francisco 53°F (11.7°C)	5	5	5	4	3	4	3	4	4	2	5	5	6	6	10	8	11	11	10	9
	2.8	2.8	2.8	2.2	1.7	2.2	1.7	2.2	2.2	1.1	2.8	2.8	3.3	3.3	5.6	4.4	6.1	6.1	5.6	5.0
Bodega Bay 52°F (11.1°C)	5	5	5	4	4	4	4	4	4	4	5	4	5	7	10	9	9	10	11	9
	2.8	2.8	2.8	2.2	2.2	2.2	2.2	2.2	2.2	2.8	2.8	2.2	2.8	3.9	5.6	5.0	5.0	5.6	6.1	5.0

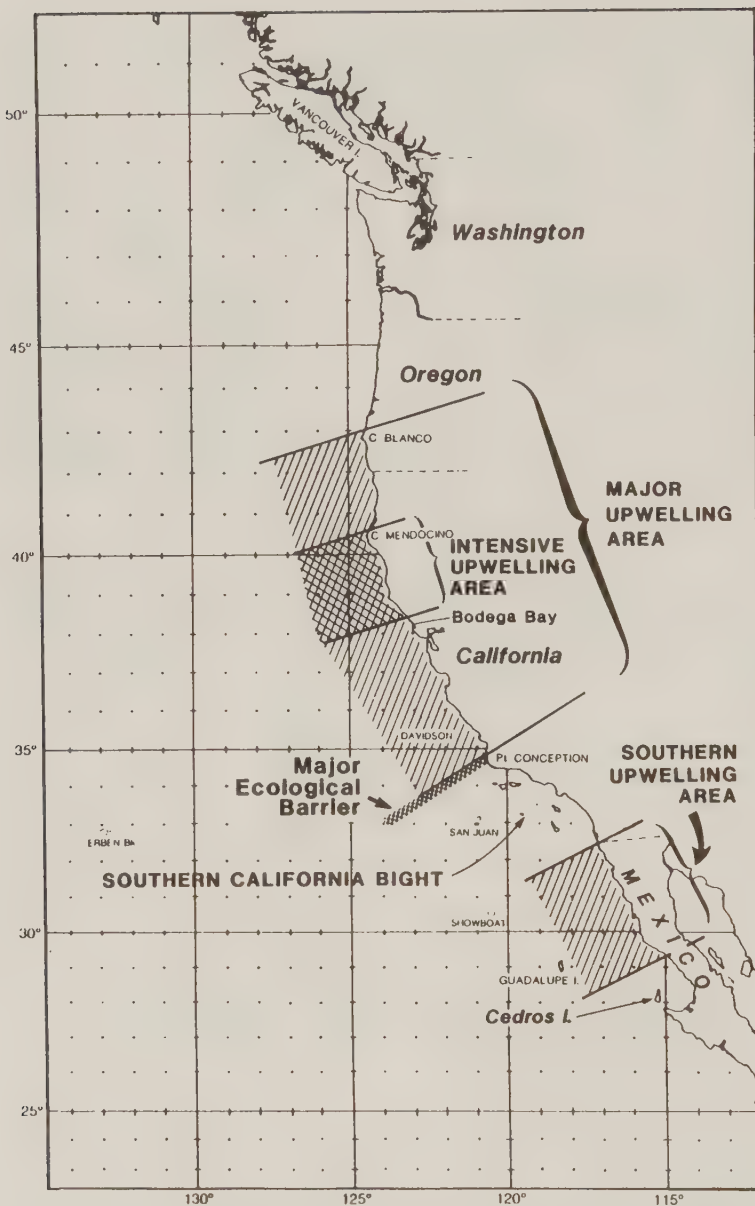


Figure 10. -- Major ecological SST barrier areas to the northward migration of subtropical and tropical coastal pelagic species.

offshore area may provide an environment that in most years inhibits the movement of the more southern species north of San Francisco.

The eastward moving North Pacific Current, toward the coasts of central Oregon, Washington, and British Columbia and into the Gulf of Alaska (the Alaska gyre), tends to moderate coastal SST's north of lat. 45°N, which are often several degrees warmer than those found off central and northern California. Once the coastal pelagic fish common to the more southern latitudes reach a point north of the major west coast upwelling area, the isotherm structure provided by the counterclockwise Alaskan gyre may enable these fishes to move northward off the coasts of Washington and British Columbia and into the Gulf of Alaska. For example, Pacific bonito were reported in the summer of 1983 off Klawock and Kodiak Island, Alaska, and Pacific barracuda off Ketchikan, and Kodiak Island. Mean SST charts for semimonthly periods developed by the National Weather Service, National Meteorological Center, were examined for the periods in 1983 when the low mean catch temperatures for yellowtail, Pacific barracuda, white seabass, Pacific bonito, and chub mackerel were geographically above lat. 52°N (Fig. 3-7). The geographical extent of the mean low catch temperature into the Gulf of Alaska area is shown in Figure 11.

Positive SST anomalies off southern California (Fig. 1) during the warm period of 1957-1958 (McGary, 1960) peaked in September 1957 and were greater by 2°F (1.1°C) in 1957 than in 1983. Since September normally has high SST's and is a high catch-rate month off southern California for many of the subtropical pelagic species, the 1957 temperature peak came at a favorable time. In the El Niño period of 1972, positive SST anomalies peaked off southern California in October, but with less intensity of 2°-4°F (1.1°-2.2°C); however, the period was still near the time that subtropical and tropical species migrate northward. In contrast, during the warming off southern California in 1983, positive anomalies peaked first in February—not a period of northward migration of tropical and subtropical species into

area to the north has within it areas of intensive upwelling that produce some of the lowest temperatures observed along the U.S. west coast. The area from north

of Bodega Bay to Cape Mendocino, Calif., is recorded as having consistently low temperatures (Squire, 1971). Sea surface temperatures in this coastal and

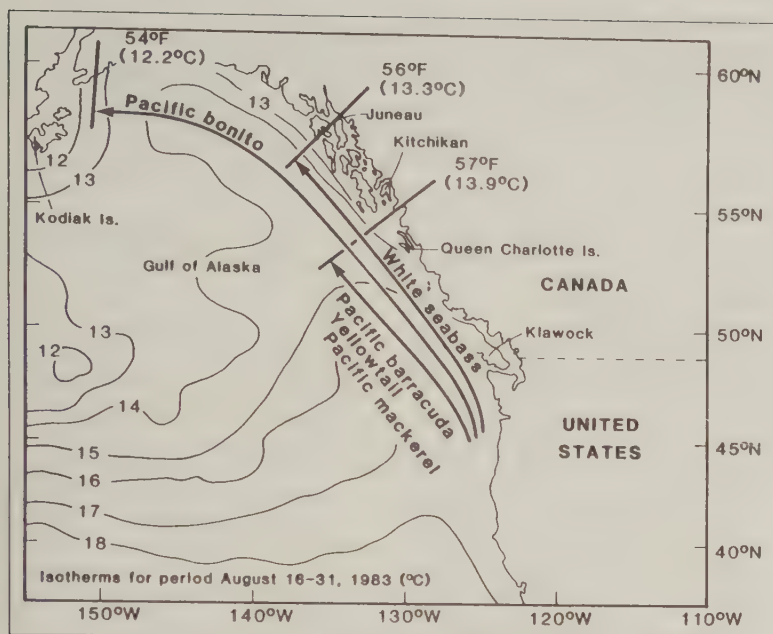


Figure 11.—Northern coastal geographical limits in 1983 of low mean catch temperature as observed off southern California for Pacific bonito, white seabass, Pacific barracuda, yellowtail, and chub mackerel.

southern California. The SST declined slightly in spring 1983 but resurged to levels of about 3°-4°F (1.7°-2.2°C) above normal from August through October, providing a sustained warm period of about 15 months during which positive anomalies of 2°F (1.1°C) or more allowed a northward extension of the distribution range for many pelagic species.

Geographical location of the temperature representing the lower limit of one standard deviation about the mean catch temperature appeared to reach its maximum northern latitudinal extent during the period 1-15 September, 1983 (see Fig. 3-7). This maximum indicated that the SST was most favorable for movement of the subtropical fishes to more northern latitudes of Oregon and Washington in early September. The geographical position of one standard deviation value below the mean was north of Point Conception for chub mackerel from July through November; yellowtail, August to October; white seabass from July through November; Pacific bonito, July through November; and Pacific bar-

racuda, June to late November.

Species common to southern California during the summer and early fall fishing season that have mean catch temperature limits indicative of a greater northward migration than yellowtail and Pacific barracuda, are the Pacific bonito (Fig. 5, 11) and white seabass (Fig. 6, 11). The geographical position of the low mean catch temperature for Pacific bonito was north of Point Conception in mid-1983 and remained further north of lat. 52°N for a longer period than did the low mean catch temperature parameter for white seabass. On the basis of monitoring in previous warming periods and in 1983, the northward movement of the Pacific bonito appears to have exceeded that for white seabass. In 1983, the tendency for northward migration was less evident for yellowtail and white seabass than for Pacific bonito and Pacific barracuda. The mean catch temperature for yellowtail and Pacific barracuda was less frequently observed at latitudes north of Cape Blanco (lat. 43°N) and at or above lat. 52°N. Chub mackerel was caught

over a wider range of temperatures than any other of the coastal pelagic species studied, and the geographical position of its low mean catch temperature (57°F or 13.9°C) was often at or above the latitude of San Francisco. Mean catch temperature values were north of Point Conception from August to 15 October, 1983. In terms of the potential for occurrence in northern latitudes, chub mackerel would rank between Pacific bonito and yellowtail. They were common from the central coast of California to British Columbia, and extended into the southern portion of Puget Sound.

The mean catch temperature at which yellowfin tuna are taken off the southwestern coast of Baja California was observed off southern California as early as August 1983 and was common there through October 15. Record-setting catches of yellowfin tuna were made during this period, in addition to good catches of skipjack tuna. Yellowfin tuna were not taken in substantial quantity west or northwest of long. 120°W (southeast of Santa Barbara, Calif.). The reason for the markedly higher catches of yellowfin tuna in 1983 than in 1957 is not apparent.

The mean catch temperature for striped marlin was first observed off southern California in August and remained off this area through 15 October 1983. Analysis of 20 years of SST and striped marlin catch data off southern California indicated an exponential increase in catch through a mean temperature of 72°F (22.2°C) (Squire, 1985). Sea surface temperature charts for the region off southern California show that temperatures are highest in the Gulf of Catalina, a part of the southern half of the Southern California Bight. Although SST's of 76°-80°F (24.4°-26.7°C) were reported in this area in September 1983, the average SST charts for this period indicate a maximum temperature of about 72°F (22.2°C). Temperatures in the normal catch areas were reported by fishermen to be considerably above the 72°F (22.2°C) maximum, and this may have resulted in a concentration of striped marlin in the northwest corner of the Southern California Bight in an area of cooler water. Excellent catches were made south of the Santa Barbara Channel Islands (near

Point Conception), along with some catches north of Point Conception near Morro Bay, Calif. The lower catch temperature limits for striped marlin off southern California (62°F or 16.7°C) extended north to the latitude of San Francisco, and catches were made in Monterey Bay and in the offshore area.

Mean catch temperatures observed during non-El Niño years for salmon off the Monterey Bay to Bodega Bay area were compared with temperatures observed in 1983. Temperatures were above optimal catch temperatures from 2° to 9°F (1.1° to 5.0°C) during the normal high catch periods and were above normal during all semimonthly periods in January through 15 October, 1983. Poor catches in the warm year of 1983 appear to parallel the occurrence of low catches during the warm years of 1957-58.

Literature Cited

- Ahlstrom, E. H. 1961. Fisheries oceanography. Calif. Coop. Oceanic Fish. Invest. Rep. 8:65-68.
- _____. 1967. Co-occurrences of sardine and anchovy larvae in the California Current region off California and Baja California. Calif. Coop. Oceanic Fish. Invest. Rep. 11:117-135.
- Anonymous. 1960. Review of the partial resurgence of the sardine fishery during the 1958-59 season. Calif. Coop. Oceanic Fish. Invest. Rep. 7:8-10.
- _____. 1969. Monthly charts of mean, minimum, and maximum sea surface temperature of the North Pacific Ocean. U.S. Naval Oceanogr. Off., Spec. Publ. 123, 58 p.
- _____. 1984. The fishery. Inter-Am. Trop. Tuna Commiss., Q. Rep., Oct.-Dec. 1983.
- Bell, F. H., and A. T. Pruter. 1958. Climatic temperature changes and commercial yields of some marine fisheries. J. Fish. Res. Board Can. 15:625-683.
- Blessner, F. 1984. The El Niño factor, West. Saltwater Fisherman 4(2):9-10.
- Brett, J. R. 1956. Some principles in the thermal requirements of fishes. Q. Rev. Biol. V. 31(2):75-87.
- Fluharty, D. 1984. 1982-1983 El Niño task force summary. Inst. Mar. Stud., Univ. Wash., June 1984, 25 p.
- Frey, H. W. 1971. California's living marine resources and their utilization. Calif. Dep. Fish Game, 147 p.
- Hubbs, C. L. 1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. J. Mar. Res. 7:459-482.
- _____. and L. P. Schultz. 1929. The northward occurrence of southern forms of marine life along the Pacific Coast in 1926. Calif. Fish Game 15:234-241.
- Jensen, A. J. C. 1930. On the influence of hydrographical factors upon the yield of the mackerel fishery in the sound. Dan. Biol. Sta. Rep. 36:71-88.
- Ketchen, K. S. 1956. Climatic trends and fluctuations in yield of marine fisheries of the Northeast Pacific. J. Fish. Res. Board Can. 13:37-374.
- McGary, J. W. 1960. Surface temperature anomalies in the central North Pacific January 1957-May 1958. Calif. Coop. Oceanic Fish. Invest. Rep. 7:147-151.
- Miller, D. J., R. Lea. 1972. Guide to the coastal marine fish of California. Calif. Dep. Fish Game, Fish. Bull. 157, 235 p.
- Miller, W. T. 1956. The possible relationship of water temperatures with availability and year-class size in the Pacific sardine (*Sardinops caerulea*). Masters Thesis, Stanford Univ., Calif., 51 p.
- Phillips, J. B. 1958. Southerly occurrences of three northern species of fish during 1957, a warm water year on the California coast. Calif. Fish Game 44:349-350.
- Radovich, J. 1960. Redistribution of fishes in the eastern north Pacific Ocean in 1957 and 1958. In Calif. Coop. Oceanic Fish. Invest. Rep. 7, p. 163-171.
- _____. 1961. Relationship of some marine organisms of the northeast Pacific to water temperatures. Calif. Dep. Fish Game, Fish. Bull. 112, 62 p.
- _____. 1975. Water temperature and fish distribution: An epilogue to the warm waters years. In Rec. Proc. 13th Pac. Sci. Cong. Aug. 18-30, 1975 Univ. B.C., Vancouver, Vol. 1, p. 264-265.
- Reid, J. L., G. Roden, and J. Wyllie. 1958. Studies of the California Current system. Calif. Coop. Oceanic Fish. Invest. Rep. 6:27-56.
- Royal, L. A., and J. Tully. 1961. Relationship of variable oceanographic factors to migration and survival of Fraser River salmon. Calif. Coop. Oceanic Fish. Invest. Rep. 8:65-68.
- Sette, O. E. 1961. Problems in fish population fluctuations. Calif. Coop. Oceanic Fish. Invest. Rep. 8:21-24.
- _____. 1969. A perspective of a multi-species fishery. Calif. Coop. Oceanic Fish. Invest. Rep. 13:81-87.
- Squire, J. L. 1971. Measurements of sea surface temperature on the eastern Pacific continental shelf using infrared radiometry. U.S. Coast Guard Oceanogr. Rep. 47 (CG 373-47), 229 p.
- _____. 1974. Catch distribution and related sea surface temperatures for striped marlin (*Tetrapturus audax*) caught off San Diego, Calif. In R. S. Shomura and F. Williams (editors), Proc. Int. Billfish Symp., Kailua-Kona, Hawaii, 9-12 Aug. 1972, Part 2, Rev. Contrib. Pap., p. 188-193. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.
- _____. 1978. Sea surface temperature distribution obtained off San Diego, California, using an airborne infrared radiometer. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-720, 30 p.
- _____. 1982. Catch temperatures for some important marine species off California. U.S. Dep. Commer., NOAA Tech. Rep. NMFS-SSR-F 759, 19 p.
- _____. 1983. Abundance of pelagic resources off California, 1963-78, as measured by an airborne fish monitoring program. U.S. Dep. Commer., NOAA Tech. Rep. NMFS, SSRF 762, 75 p.
- _____. 1985. Isotherm patterns off northwestern Mexico relative to the catch of striped marlin *Tetrapturus audax*, off southern California. Mar. Fish. Rev. 47(3):43-47.
- Uda, M. 1957. A consideration of long years trend of fisheries fluctuation in relation to sea conditions. Bull. Jpn. Soc. Sci. Fish. 23:368-372.
- _____. 1961. Fisheries oceanography in Japan, especially on the principles of fish distribution, concentration, dispersal and fluctuation. Calif. Coop. Oceanic Fish. Invest. Rep. 8:25-31.
- Young, P. H. 1969. The California party-boat fishery 1947-1967. Calif. Dep. Fish Game, Fish. Bull. 145, 91 p.
- Walford, L. A. 1931. Northward occurrence of southern fish off San Pedro in 1931. Calif. Fish Game 17:401-405.

Striped Marlin, *Tetrapturus audax*, Migration Patterns and Rates in the Northeast Pacific Ocean as Determined by a Cooperative Tagging Program: Its Relation to Resource Management

JAMES L. SQUIRE

Introduction

Since billfish cannot be captured in large numbers to study movements through tagging studies, marine anglers who will tag and release fish provide an effective, alternate way to obtain information on migration patterns. Billfish tagging by marine anglers in the Pacific began in the middle 1950's when tagging equipment, distributed to anglers by the Woods Hole Oceanographic Institution's (WHOI) Cooperative Marine Game Fish Tagging Program for tagging tunas and billfish in the Atlantic, was transported to fishing areas in the Pacific.

Sailfish, *Istiophorus platypterus*, were first tagged by billfish anglers in the northeast Pacific in 1954, and striped marlin, *Tetrapturus audax*, were first tagged in 1957. In 1961, black marlin, *Makaira indica*, were first tagged in the southwest Pacific (Coral Sea), and in 1963 blue marlin, *Makaira nigricans*, were tagged in the central Pacific (Squire, 1974). Cooperative billfish tagging programs with rod-and-reel anglers

were developed to obtain an understanding of migratory patterns that could be useful in developing management plans for Pacific billfish stocks.

In 1963, the U.S. Fish and Wildlife Service's Pacific Marine Game Fish Research Center, Tiburon Marine Laboratory, Tiburon, Calif., under the U.S. Department of Interior, assumed responsibility from WHOI for support of the Cooperative Marine Game Fish Tagging Program in the Pacific area. In 1970 a reorganization transferred the Tiburon Laboratory and the tagging program to the National Oceanic and Atmospheric Administration's National Marine Fisheries Service (NMFS) in the U.S. Department of Commerce. From 1963 to 1970 the State of California's Department of Fish and Game (CDFG) also provided tags to a select group of cooperating anglers to tag striped marlin (Squire, 1974).

The angler tagging programs have now accounted for nearly all the tagged billfish in the Pacific at a relatively modest cost compared to that which would have been incurred had the same fish been caught and tagged by more efficient longline gear from research vessels. These billfish were tagged mainly in areas that support active recreational billfish fisheries.

There is a major recreational fishery for striped marlin in the northeastern Pacific centered about the southern tip of Mexico's Baja California Sur peninsula, and it is very important to the economy of that area (Talbot and Wares, 1975). High

catch rates are recorded in this area and surveys show the catch per angler day has ranged from 0.3 to 0.8 striped marlin since 1969 (Squire, 1986). Some striped marlin are also landed at Mazatlán, Mex., and others are occasionally taken off other west coast ports of Mexico and off Central and South America. High catch rates are observed again off Ecuador. In the northeast Pacific, high catch rates for striped marlin are recorded from January to March off Mazatlán, Mex., and later in the year (April-October) about the southeastern tip of the Baja California peninsula (Eldridge and Wares, 1974). The U.S. recreational fishing fleet off southern California lands striped marlin from July through October, with catches usually peaking in September; this area is the northern limit of the recreational fishery in the eastern Pacific.

Longline fishing for billfish and tunas has been conducted in the eastern Pacific (east of long. 130°W.) since the late 1950's (Suda and Schaefer, 1965) and in the northeastern Pacific, where it has targeted on striped marlin, sailfish, and swordfish, *Xiphias gladius*, since 1963 (Joseph et al., 1974). The catch rate for striped marlin in the high catch rate areas of the northeastern Pacific has declined from about 18 fish per 1,000 hooks fished in the early 1960's to about 9-11 fish per 1,000 hooks fished in 1980 (Anonymous, 1962-80). This decline came during the time tagging was conducted. Despite the substantial catch rate decline since the beginning of the fishery, the rate is among the highest in the Pacific, and this longline fishery provides in excess of 80 percent of the billfish tags recovered. From early 1977 to 1980 longline fishing for billfish and

ABSTRACT—Migration patterns and rates for striped marlin, *Tetrapturus audax*, tagged and recaptured in the northeast Pacific Ocean during 1957-81 are reported by time period and analyzed. Few long-range migrations and no trans-Pacific migrations were observed. Comparisons are made with other types of physical and biological data that might indicate seasonal movement (i.e., longline catch rates, areas of striped marlin spawning, movement of thermocline depth relative to fishing success). A tentative hypothesis describing the seasonal movement of striped marlin in the northeast Pacific and the total eastern Pacific is also proposed and presented in graphic form.

James L. Squire is with the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038

tunas was prohibited by the Government of Mexico within its 200-mile economic zone. The highest catch rates for striped marlin are about the southern tip of Baja California Sur, within the 200-mile zone. Joint-venture longline operations were resumed in 1980, providing a source of striped marlin tag recoveries.

Between 1964 and 1981, 155 tagged striped marlin were recovered—the majority by foreign commercial longline vessels. From recovery records it is possible to reconstruct migration patterns and rates. In this study I discuss the factors affecting tagging and recovery as they relate to migration, and the implications of the results for fishery management.

Tagging Methods and Results

Methods

According to the tagging instructions, when the billfish is brought alongside the boat the angler is to insert the dart tag beside the dorsal fin. Descriptive literature illustrating the suggested point of tag insertion is distributed with the tagging equipment. Because tagging of a large active billfish that cannot be lifted from the water or partially immobilized is a difficult task, it is probable that many tags have not been inserted as recommended.

When the tagging equipment is distributed to the angler, the tags are attached to a postcard (tag report card) which indicates the serial number of the tag (Fig. 1). After tagging a fish, the angler is requested to complete the tag information card with the date, location, species, estimate of marlin's weight and length, and the tagger's name and address; the angler is requested to return the card to the organization issuing the tag.

Tags used by billfish anglers participating in the Cooperative Marine Game Fish Tagging Program were described by Squire (1974). Four types of tags have been used for tagging striped marlin in the northeast Pacific Ocean (Fig. 1). For tagging conducted under NMFS sponsorship, less than 1 percent of the striped marlin were tagged with type "A" tags. About 7 percent were type "B" or FT-1, 37 percent type FM67, and 56 percent type FH69 or "H" type. The percentage

Figure 1.—Dart tags and tag report card used by the NMFS for the cooperative tagging program for tagging striped marlin in the northeast Pacific Ocean.

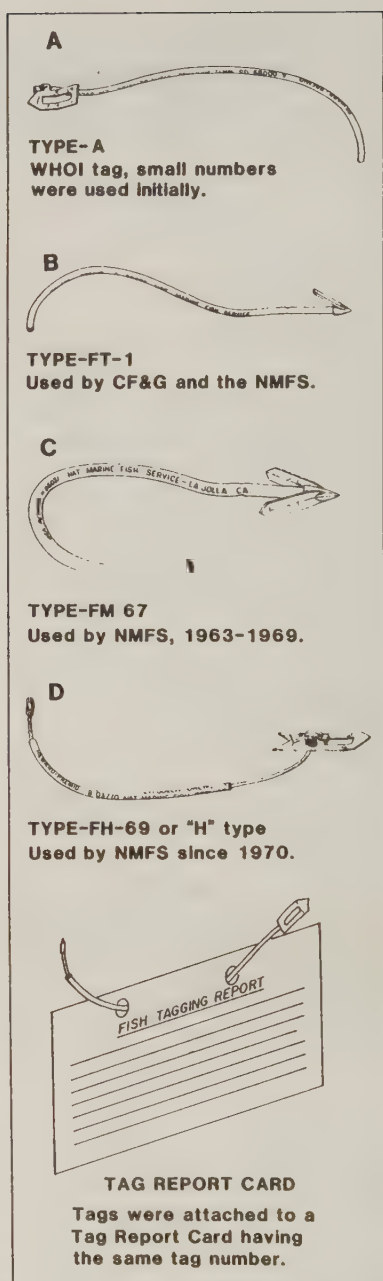
Table 1.—Annual number of striped marlin tagged by Cooperative Marine Game Fish Tagging Program Agency, 1957-81.

Year	CDFG	WHOI	NMFS			Total
			Calif- lornia	Baja Calif Sur	Mazatlán	
1957		17	—	—	—	17
1958		13	—	—	—	13
1959		10	—	—	—	10
1960		2	—	—	—	2
1961		87	—	—	—	87
1962		76	—	—	—	76
1963	18	942	6	7	—	973
1964	329	113	9	243	8	702
1965	253	52	3	208	7	523
1966	186	47	13	365	15	626
1967	107	31	14	432	166	750
1968		29	17	749	59	854
1969	1	5	12	406	39	463
1970	2	6	24	617	54	703
1971		9	13	827	7	856
1972		—	7	804	1	812
1973		—	2	344	3	349
1974		—	54	603	3	660
1975		—	15	473	1	489
1976		—	46	576	9	631
1977		—	37	315	—	352
1978		—	24	557	—	581
1979		—	42	458	—	500
1980		—	22	1,142	—	1,164
1981		—	60	641	—	701
	896	1,439	420	9,767	372	12,894

of tag types used in the three areas of tagging was similar to the above distribution percentages, with one exception. A low percentage (4 percent) of FH69 tag were used at Mazatlán, due to a substantial reduction in tagging effort there in the early 1970's, at about the time the FH69 tag was introduced.

Tagging Results

Between 1957 and 1981, 12,894 striped marlin were reported tagged in the northeast Pacific. This number represents only those tags for which a tag card was returned to the agency distributing the tags. Table 1 gives the number of striped marlin tagged by agencies that have provided tags to cooperating marine anglers. During 1963-81 the NMFS program accounted for 10,559 striped marlin tagged or 82 percent of the total number tagged.



Maximum tagging effort was in 1980 (1,164 striped marlin tagged), and lowest effort in 1974 (349 striped marlin

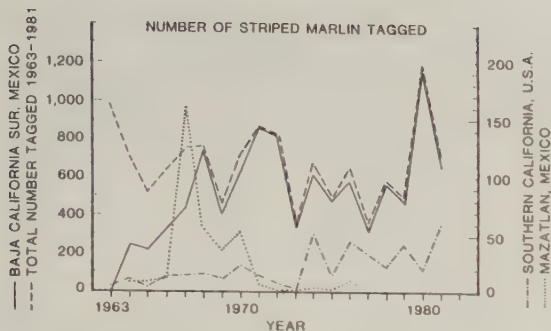


Figure 2.—Distribution of tagging effort, by year, for striped marlin off Mazatlán, Baja California Sur, and southern California, 1963-81.

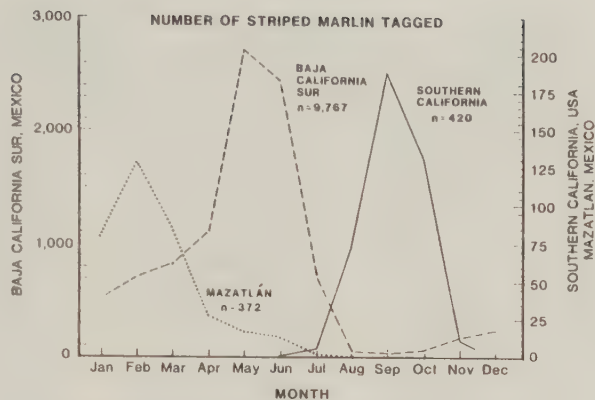


Figure 3.—Distribution of NMFS tagging effort, by month for tagging off Mazatlán, Baja California Sur, and southern California, 1963-81.

tagged); average tagging rate for 1963-81 was 668 striped marlin per year.

Distribution of tagging effort for the three major areas of tagging is given in Figures 2 and 3. Tagging effort increased off Mazatlán and Baja California Sur, Mex., in the middle 1960's. Through 1981, tagging effort levels ranged from 350 to 1,200 fish per year for Baja California Sur, and 30-80 fish for southern California.

The tagging program is a cooperative one and is dependent upon the active support of the anglers. Thus tagging frequency can fluctuate greatly, depending upon fishing success; tagging will be maximum during the peak of the fishing season and during seasons having better than average catches, and tagging will tend to be centered in specific geographical areas. Tagging of striped marlin in the northeast Pacific during any one year is not distributed randomly in time. High catch rate periods are evident for each of the three tagging areas. Figure 3 illustrates the timing of the releases for each of the three major tagging areas. The timing of tagging off Mazatlán and southern California is directly related to striped marlin availability occurring only during specific months. Striped marlin are available about the southern tip of Baja California Sur during most months of the year; however, because of a climate of high temperatures and humidity during the mid-summer through the fall there is much less fishing effort, and therefore less tagging.

There was little opportunity to recover

tagged striped marlin in the eastern Pacific before the early 1960's. Prior to that time the Japanese longline fishery was expanding into the eastern Pacific, but the fishery had not yet concentrated in the northeast Pacific for the specific purpose of fishing striped marlin, sailfish, and swordfish. The recreational fishery continued to develop in the northeast Pacific but with a lower total estimated catch compared with current catches of an estimated 4,000-6,000 striped marlin per year. With the establishment in the early 1960's of an active commercial longline fishery in the northeast Pacific, the opportunity to recover tagged billfish increased (Ueyanagi, 1974). The Japanese longline fishery has recorded catches in the eastern Pacific (east of long. 130°W) of from 40,000 to 338,000 striped marlin annually during 1962-81. In 1963, the Japanese longline fishery for striped marlin, operating off the Baja California Sur peninsula (the major area of tagging), increased substantially and remained at a high level of effort until early 1977; catches from this area averaged about 30,000 striped marlin a year (Anonymous, 1962-80).

Recovery Rates of Tag Types

Of the striped marlin reported tagged during 1968-81, 12,689, 155 tags were returned for an overall return rate of 1.2 percent. The highest annual recovery rate

was recorded in 1967—a 2.8 percent rate of recovery for 750 striped marlin tagged. The 1970 fishery (703 fish) yielded the second highest recovery rate—2.3 percent. These higher rates were recorded using FM67 tags. The recovery rate of the all-plastic double-barbed FM67 tag was 1.6 percent for 4,236 tags used. For 5,325 FH69 ("H" type) tags used, the recovery rate was 1.0 percent. A 38 percent greater tag return rate occurred with the FM67 tag compared with the FH69 tag.

Release and tag recovery data are given in Table 2. The foreign commercial longline fleet has provided 77 percent of the striped marlin tag recoveries for the NMFS program, billfish anglers have accounted for 16 percent, and the remainder (7 percent) have come from either other types of commercial fishing boats or tags washed ashore.

Considerable variation in recovery rate by year was observed between tag types. Table 3 gives the total number of recoveries by year and tag types for 1963-81. Table 4 gives striped marlin tag recovery rates by year tagged and by the two major tag types used by NMFS—FM67 and FH69.

Angler Estimated Weight Data

The angler, upon tagging a billfish, is asked to record the estimated length and weight of the tagged striped marlin on the

Table 2.—Striped marlin tagging and recapture data, 1963-81.

Year	Tagging data				Recapture data		
	SWFC no.	Location ¹	Tagger	Date	Vessel or person	Distance ² and direction from pt. of tagging	Days to recapture
1963	1	B	R. Fisher	6/6/63	Matsumoto maru #2	1,153/S	71
1964	2	E	G. Daley	2/24/64	Tosui maru #10	510/NW	59
1964	3	B	G. Myette	2/10/64	Okiya maru #8	162/SE	82
1964	4	B	B. Wilson	2/10/64	Seisho maru #11	140/SSW	56
1964	5	B	D. Cox	5/2/64	Kyowa maru #2	90/SSE	14
1964	6	B	C. Herrguth	5/26/64	Fukukyu maru #5	257/S	91
1964	7	A	C. Brignelli	10/6/64	Kyowa maru #2	668/SE	26
1964	8	A	J. Koons	10/20/64	(Japanese longliner)	621/SE	34
1964	9	A	M. Freis	9/19/64	(Japanese longliner)	668/SE	87
1964	10	B	B. Hehr	2/7/64	(Japanese longliner)	320/SSW	154
1964	11	B	Unknown	3/15/64	Gemini/W. Kalayjah	3/SE	40
1965	12	B	H. Chappell	3/1/65	Unknown (Mexican boat)	0 n.mi.	13
1965	13	B	J. Kott	6/10/65	Hakuyo maru #28	108/S	47
1965	14	B	C. Brignall	6/25/65	Shoei maru #7	116/NE	46
1965	16	B	R. Fredman	5/19/65	Bunyo maru #1	210/NW	82
1965	18	B	B. Nicholes	5/18/65	Syoei maru #12	361/S	64
1965	19	A	J. Mathiesen	9/6/65	Fuji-sei maru #3	560/SE	59
1966	20	B	R. Switzer	4/29/66	Keiluku maru #3	155/SE	13
1966	21	B	P. MacMahon	5/6/66	Keiluku maru #3	190/SE	6
1966	22	B	R. Farley	3/15/66	Keiluku maru #3	198/SE	61
1966	23	B	E. Spainard	5/3/66	Keiluku maru #3	186/SE	17
1966	24	B	O. Spainard	5/4/66	Keiluku maru #3	224/SE	19
1966	25	B	T. Munteen	3/27/66	Keiluku maru #3	226/SE	67
1966	26	B	Unknown	5/15/66	Syoei maru #7	138/S	110e ³
1966	27	D	G. Heimpel	3/10/66	Syoei maru #7	252/W	146
1966	28	B	F. Bennett	4/14/66	(Sportboat) P. Testa	21/ESE	63
1966	30	B	P. Macklitz	5/6/66	Kyowa maru #2	161/SW	199
1966	31	B	N. Schwin	4/7/66	Kyowa maru #2	63/S	225
1966	32	B	Unknown	Unknown	Kyowa maru #2	70/S	
1966	40	B	C. Hopton	4/15/66	Keiluku maru #7	100/NW	483
1967	34	B	H. Fink	6/9/67	(Sportboat) J. Ross	64/SW	18
1967	36	B	Unknown	2/13/67	Kaime maru #18	3,120/W	120
1967	37	B	J. Ribeiro	6/29/67	Koan maru #18	260/S	55
1967	38	D	G. Lyons	1/10/67	Keiluku maru #7	172/W	239
1967	39	D	L. Nelson	2/14/67	Keiluku maru #7	226/SW	213
1967	41	D	J. Sax	3/11/67	Kyowa maru #2	111/SW	45
1967	42	B	E. Horn	3/25/67	Kyowa maru #2	155/SE	30
1967	43	D	W. Milan	1/18/67	Kyowa maru #2	232/W	101
1967	44	D	M. Mernick	3/9/67	Kyowa maru #2	210/W	40
1967	45	D	K. Blacker	3/9/67	Kyowa maru #2	103/W	91
1967	46	D	H. Falt	6/21/67	Kyowa maru #2	233/W	28
1967	47	D	R. Daniels	3/3/67	Kyowa maru #2	276/W	206
1967	48	B	H. Ness	9/25/67	Kyowa maru #2	212/S	111
1967	49	D	B. Heimpel	7/14/67	Dyowa maru #2	169/W	88
1967	50	C	J. Binney	8/18/67	Dyowa maru #2	380/S	46
1967	51	D	Unknown	2/2/67	Kyowa maru #2	130/SW	93
1967	53	B	Unknown	4/15/67	Shiyoei maru #12	280/S	150e
1967	54	B	Unknown	4/10/67	Shiyoei maru #12	290/S	150e
1967	56	B	Unknown	Unknown	Sportboat/W. Werner, 2/2/68	Appx. same area	
1967	62	A	B. Devere	9/9/67	Kensei maru #26	2,090/WSW	179
1967	64	D	M. Olivetti	2/14/67	Syoei maru #12	285-SW	514
1968	57	B	J. McAieer	1/16/68	Anei maru #3	155-SE	27
1968	59	B	Unknown	Unknown	Anna Belle/T. Locke	10 n.mi.	
1968	61	B	G. Knudsen	3/16/68	Syoei maru #7	75/E	75
1968	65	B	R. Honeycutt	3/7/68	Chokyu maru #12	278/SW	183
1968	66	B	J. Warren	6/28/68	Hokucho maru #18	140/SW	65
1968	67	B	B. Enyart	4/26/68	Huckuho maru #18	241/S	166
1968	68	B	J. McTee	3/25/68	Fuku maru #8	374/SE	133
1968	70	B	R. Fansett	6/30/68	Fuku maru #8	366/S	40
1968	71	B	J. McDonald	7/22/68	Genkai maru #18	125/NW	43
1968	72	B	J. Grigsby	6/13/68	Genkai maru #18	285/SW	95
1968	73	A	D. Daley	10/5/68	(Beach) R. Armstrong	70-SE	
1969	75	B	B. Constantine	2/27/69	Sportboat/R. Jensen	12/N	1
1969	79	B	R. Taylor	2/2/69	(Japanese longliner)	285-SW	147
1969	80	B	L. Griffin	5/5/69	(Beach)/V. Wares	20 n.mi.	
1969	81	B	D. Sansome	2/11/69	Chokyu maru #12	81/NE	157
1969	108	B	P. McVay	12/29/69	Chokyu maru #12	156/SE	5
1969	119	D	Unknown	4/21/69	Shoei maru #38	13/W	22
1970	82	D	B. Heimpel	1/13/70	Chokyu maru #12	32/S	5
1970	87	B	J. Smith	3/1/70	Keiluku maru #7	120/E	20
1970	91	B	R. Hodgden	2/5/70	Fukuku maru #18	98/E	20
1970	93	B	R. Fadem	3/5/70	Keiluku maru #7	53/NNW	74
1970	94	B	C. Errega	5/28/70	Fukuku maru #18	195/S	36
1970	99	B	B. Ashby	1/22/70	Charter boat/T. Schiltz	210/E	57
1970	100	Unk	D. Stone	Unknown	Shoei maru #12		
1970	101	B	Unknown	3/70e	Kyowa maru #2	180/S	40e
1970	103	A	R. Naltzger	8/2/70	(Beach)/D. Mullis	60/SE	
1970	104	B	W. Marcusson	6/16/70	Azuma maru #31	120/SW	49
1970	105	B	G. Robinson	5/26/70	Chokyu maru #15	60/S	135
1970	106	B	R. von Ottow	2/9/70	Chokyu maru #15	95/NW	225

Continued on next page

Table 3.—Recapture of striped marlin by year and tag.

Year	Recovery by tag type					Percent recovery
	A	FT-1	FM67	FH69(H)	Total	
1963	1				1	0.1
1964	1	4	5		10	1.4
1965	1		5		6	1.1
1966		2	11		13	2.1
1967		1	20		21	2.8
1968			12		12	1.4
1969			6		6	1.3
1970	1	15			16	2.3
1971		1		1	2	0.2
1972				6	6	0.7
1973				2	2	0.6
1974				8	8	1.2
1975				4	4	0.8
1976				5	5	0.8
1977				3	3	0.8
1978				2	2	0.3
1979				3	3	0.6
1980				23	23	1.9
1981			1	11	12	1.7
Totals	3	8	76	68	153 ¹	

¹Total = 155 (2 recaptures not identifiable as to year tagged)

Table 4.—Striped marlin tag recapture rates by year and tag (FM-67 and FH-69).

Year	FM 67			FH-69 ("H")		
	Tagged (no.)	Recaptured (no.)	Recaptured (%)	Tagged (no.)	Recaptured (no.)	Recaptured (%)
1963	9	0	0.0			
1964	232	5	2.15			
1965	200	5	2.50			
1966	370	11	2.97			
1967	683	18	2.53			
1968	818	10	1.22			
1969	450	6	1.33			
1970	646	14	2.16			
1971	639	1	0.01	194	1	0.05
1972	76	0		698	6	0.85
1973	8	0		334	2	0.59
1974	31	0		597	8	1.34
1975	7	0		481	2	0.41
1976	7	0		623	5	0.80
1977	5	0		347	3	0.86
1978				580	2	0.34
1979				500	3	0.60
1980				1,163	23	1.97
1981	1	1	100	701	10	1.42
Over-all	4,236	71	1.57	5,325	55	1.03

tagging information card which is attached to the tag (Fig. 1). Because of their size and active nature, marlin caught by rod and reel are not removed from the water at the time of tagging, and thus only an estimate of weight is possible. Very few anglers gave estimates of length, although 96 percent of the tag cards included estimates of weights. The average estimated weight by year for

Table 2.—Continued.

Year	Tagging data			Recapture data		
	SWFC no.	Location ¹	Tagger	Date	Vessel or person	Distance ² and direction from pt. of tagging
1970 107	B		J. Fiol	5/9/70	Shinko maru	70/E
1970 109	B		J. Recchardt	2/15/70	Chokyu maru #12	93/ESE
1970 110	B		C. Shattuck	3/20/70	Chokyu maru #12	125/SE
1970 111	D		B. Heimpel	Unknown	Chokyu maru #12	30/SW
1970 115	B		K. Nelfoney	3/18/70	Sportboat/W. Schreiner	110/NE
1971 117	B		G. Bruns	5/5/71	Gonei maru	213/NW
1971 118	A		H. Witherspoon	8/20/71	Kosho maru #11	675/SE
1972 121	B		J. Van Hove	4/22/72	Sportboat/A. Alvarez	<5 n.mi.
1972 126	B		W. Benson	5/1/72	Sportboat/G. Welton	70/SW
1972 138	B		A. Selby	5/19/72	Fukuyu maru #32	95/SW
1972 139	B		T. Huls	6/2/72	Fukuyu maru #32	240/NW
1972 197	B		R. Ayres	6/17/72	Keifuku maru #5	75/NW
1973 147	B		J. Birtcher	1/20/73	Kyowa maru #12	107/NE
1973 191	B		D. Rivoli	5/31/73	Kyowa maru #11	110/S
1974 187	B		Unknown	6/19/74	Chokyu maru #11	200/SW
1974 188	B		H. Shaw	5/27/74	Chokyu maru #11	105/SE
1974 189	B		Unknown	1/26/74	Chokyu maru #11	70/SE
1974 192	B		H. Moss	6/24/74	Kyowa maru #23	150/W
1974 193	B		Unknown	6/74	Kyowa maru #23	105/W
1974 194	B		B. Guenter	6/3/74	Kyowa maru #23	50/NE
1974 195	B		F. Scroggs	6/8/74	Chokyu maru #12	50/E
1974 196	B		T. McConville	6/9/74	Keifuku maru #5	55/NW
1974 224	B		I. Lewis	5/13/74	Chokyu maru #25	340/S
1975 230	B		P. Sadir	7/28/75	Sportboat/C. Taylor	180/SE
1975 263	B		C. Weiner	6/23/75	Sportboat/E. Landsaw	<5 n.mi.
1976 215	B		J. Carpenter	5/24/76	Keifuku maru #12	300/SW
1976 221	B		C. Bradfield	4/6/76	Kyowa maru #28	15/S
1976 225	B		Unknown	5/19/76	Chokyu maru #25	280/S
1976 229	B		A. Jensen	5/30/76	(Marlin on beach)	B/W
1976 247	A		E. Martin	11/11/76	Kotoshiro maru #15	2,520/S
1977 248	B		H. Consley	5/31/77	Sportboat/H. Sherman	3 n.mi.
1977 276	A		E. Martin	9/3/77	Sportboat/S. Nesbitt	35/E
1977 277	A		R. Barrett	10/12/77	Sportboat/C. Huslar	83/SE
1978 285	B		Unknown	6/78	El Indomable (tuna seiner)	60/SE
1978 306	B		F. Gilbert	12/30/78	Sportboat/L. Clinkenbeard	20/NE
1979 283	B		P. Locke	6/1/79	Fukuyu maru #32	390/SW
1979 284	B		T. Sheehan	5/1/79	Fukuyu maru #32	390/SW
1979 291	B		Unknown	4/79	Sportboat/J. Clarke	10/SE
1980 299	B		W. Jossey	3/28/80	Horso maru #21	207/S
1980 300	B		J. Collins	12/2/80	Hosyo maru #21	110/S
1980 301	B		N. Ruston	3/15/80	Chidori #86	110/SSW
1980 302	B		A. Williamson	4/14/80	Chidori #86	120/SW
1980 303	B		J. Crowson	7/8/80	Chidori #86	240/W
1980 304	B		L. Schonert	10/14/80	Chidori #86	230/W
1980 305	B		S. Stevenson	5/20/80	Fukutoku maru #18	720/SE
1980 307	B		M. Bryant	6/9/80	(Commercial diveboat)	800/NW
1980 308	B		K. Johnson	5/9/80	Japanese longliner	80/SSW
1980 309	B		J. Cunningham	5/19/80	Japanese longliner	105/SSW
1980 314	B		J. Lee	6/30/80	Sportboat/M. Barks	70/SE
1980 315	B		S. Jacobson	4/9/80	Japanese longliner	250/S
1980 316	B		J. Brandes	4/9/80	Japanese longliner	300/S
1980 318	B		Unknown	7/15/80	Sportboat/M. Brett	<5 n.mi.
1980 319	B		Unknown	5/80	Sportboat/Unknown	<5 n.mi.
1980 323	B		L. Wiczai	7/15/80	Hosyo maru #21	410/SW
1980 327	B		H. Kameron	4/2/80	Sportboat/E. Bishop	12/SW
1980 328	B		C. Ackerman	5/23/80	Sportboat/R. Fraser	60/S
1980 329	B		H. Kameon	7/17/80	Sportboat/E. Cohen	60/SW
1980 334	B		N. Yoshihara	5/6/80	Sportboat/A. Aguayo	180/SE
1980 342	B		R. Martin	6/13/80	Chidori #88	260/NW
1980 343	B		E. Clark	6/5/80	Chidori #88	260/NW
1980 344	B		T. Gillen	12/26/80	Chidori #7	240/S
1981 322	A		C. Herberls	8/30/81	Sportboat/B. Feldhorn	50/E
1981 324	B		Unknown	Unknown	Sportboat/E. Miller	<5 n.mi.
1981 325	B		J. Brown	2/28/81	Sportboat/G. Carter	<5 n.mi.
1981 326	B		N. Braemer	4/4/81	Sportboat/F. Appling, Jr.	12/E
1981 330	B		P. Gillen	1/5/81	Sportboat/T. Eillen	20/E
1981 335	Unk. ⁴		Unknown	Unknown	Korean longliner, 12/24/81	
1981 336	B		M. Abbott	12/26/81	Korean longliner	155/S
1981 337	B		P. Torre	6/15/81	Hosyo maru #21	360/S
1981 338	B		K. Delieore	10/23/81	Hosyo maru #21	240/NW
1981 339	B		E. Martin	11/30/81	Hosyo maru #21	241/NW
1981 340	B		D. Lyddon	7/2/81	Mosyo maru #21	360/S
1981 341	-		Unknown	Unknown	Hosyo maru #21	
1981 345	A		E. Martin	9/25/81	Fukuyu maru #32	600/SE
1981 346	B		W. Feldhorn	3/9/81	Fukuyu maru #32	30/W

¹A = Southern California, B = Baja California Sur, C = Guaymas-Kino area, D = Mazatlan, and E = Acapulco

²Distance is listed in nautical miles

³e = estimate.

⁴Unk. = unknown.

Table 5.—Average estimated weight for striped marlin tagged off Mazatlan and Baja California Sur, Mexico and Southern California, U.S.A., by year as recorded on the tag card report. Weights in parentheses represent the yearly average weight of landed striped marlin as recorded by the Balboa Angling Club, Balboa, California, and the Marlin Club, San Diego, California.

Year	Mazatlan	Southern California	Baja California Sur,
1963		135.0 (132.8)	127.8
1964	145.0	127.8 (134.9)	150.6
1965	147.1	126.7 (141.6)	136.1
1966	125.7	131.9 (129.1)	149.1
1967	117.1	130.4 (128.4)	137.7
1968	127.7	143.8 (136.8)	146.0
1969	117.9	150.0 (146.3)	132.1
1970	101.2	115.4 (138.8)	133.7
1971	106.6	132.2 (144.6)	125.9
1972	135.0	142.9 (146.4)	131.5
1973	146.7	125.0 (149.1)	135.6
1974	140.0	133.4 (144.4)	138.4
1975	160.0	88.0 (151.7)	143.2
1976	159.9	139.1 (142.6)	154.8
1977		135.5 (153.2)	148.3
1978		140.3 (148.0)	150.6
1979		142.7 (145.6)	138.6
1980		135.5 (153.2)	133.9
1981		166.2	144.7

striped marlin tagged off southern California, Baja California Sur, and Mazatlan is given in Table 5.

Longline vessels sometimes submitted weight data on recaptured marlin and occasionally biological information. A total of 74 striped marlin recoveries had usable weight data. The weights from the commercial longline fishery were with the bill and portion of head removed at about the area of eye orbit, and less gills and internal organs. The reported or dressed weight must therefore be increased by a factor of 1.2 to give the approximate round weight of the fish.

I compared the estimated weights at tagging and their calculated weights at recovery within release time periods; the results are given in Figure 4. For a release time of 0-60 days, the average recovery weight of 31 marlin was 0.3 kg less than the initial weight estimated by the angler at tagging. Variation is extensive between tag and recovery weights for 0-60 days, ranging from an overestimate of 12.7 kg (28 pounds) to an underestimate of 19.0 kg (42 pounds). For recoveries made 61-120 days after release, the average recovery weight was 1.5 kg (3.3 pounds) less than had been estimated by the angler. Weight at recovery would be expected to increase as time of recovery increased. Average weight estimated at time of tagging compared with average

weight at recovery appears to show a positive growth increase for the recovery period 121-240 days after tagging. On Figure 4, only 44 percent of the recoveries (30 fish) showed an increase in weight and 56 percent (38 fish) were reported caught at weights less than estimated at tagging. Five recoveries (7 percent) indicated the same weight as tagged, some having release times of 1-2 years. These data indicate that angler estimated weight data lacks the precision necessary for striped marlin growth studies. Similar conclusions were made for black marlin resulting from our Coral Sea studies (Squire and Nielsen, 1983).

Migratory Patterns and Rates

The season and geographical locations of tagging must be considered in evaluating the migratory patterns and rates determined from tagging results. Striped marlin occur throughout the Pacific Ocean between about lat. 45°N to 35-40°S and are common to the tropical and temperate waters of the Pacific and Indian Oceans (Fig. 5). Based on longline catch data, the distributional pattern of this species in the Pacific is horseshoe-shaped with the base located along the central American coast (Nakamura, 1974). Striped marlin tagging in the northeast Pacific Ocean has been concentrated in two areas about the southern tip of Baja California: Off Cabo San Lucas and about 60 miles to the northeast off Bahía de Palmas in the Gulf of California (Fig. 5). Most of the striped marlin were tagged in the Bahía de Palmas area from April to August. Only a few striped marlin have been tagged in the Gulf of California north of Bahía de Palmas. Other areas of tagging were off Mazatlán from January through March, and off the southern California coast from August to October (Fig. 3).

Few long-range recoveries were made. Only two marlin tagged off Mexico were recovered more than 1,000 n.mi. from the point of tagging (1.3 percent of the recoveries). One recovery was made 1,560 n.mi. south of the Baja California peninsula; the other recovery was made about 200 n.mi. southwest of the Hawaiian Islands. For southern California tagging, the majority of recoveries were off or south of the Magdalena Bay area with two of the eleven recoveries greater than

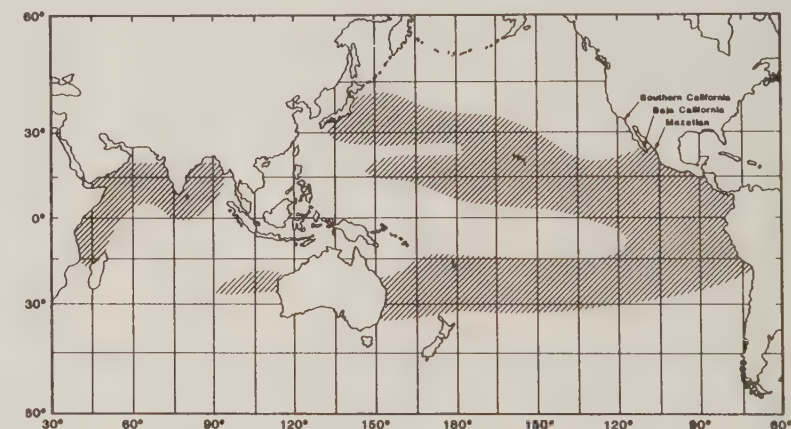


Figure 5.—Distribution of good fishing grounds for striped marlin, based on catch data from Japanese longline fishery during 1964-69 (from Nakamura, 1974).

2,000 n.mi. from the tagging point. Of the three marlin recovered off southern California, two were tagged off southern California about 1 year before recovery, and the other had been tagged about the tip of Baja California Sur 130 days before recovery.

Direction of Migration

Locations of tagging, recovery, and mean bearing direction in degrees (True) of recovery from point of tagging are

given in Figures 6-9 for time-at-large periods 0-60 days, 61-120 days, 121-240 days, and 241 days-1 year for striped marlin tagged off Baja California Sur, and Mazatlán. Figure 10 gives tagging and recovery locations for striped marlin tagged off southern California. From the tag and recovery geographical plots in Figures 6-10 it appears that all migration is radiating outward from a geographically localized point of tagging, and that the tagging location is the "center" of dis-

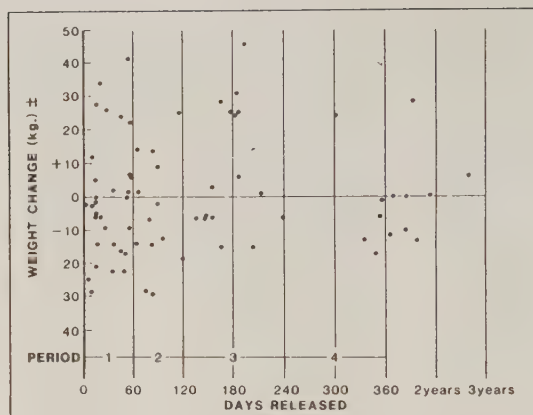


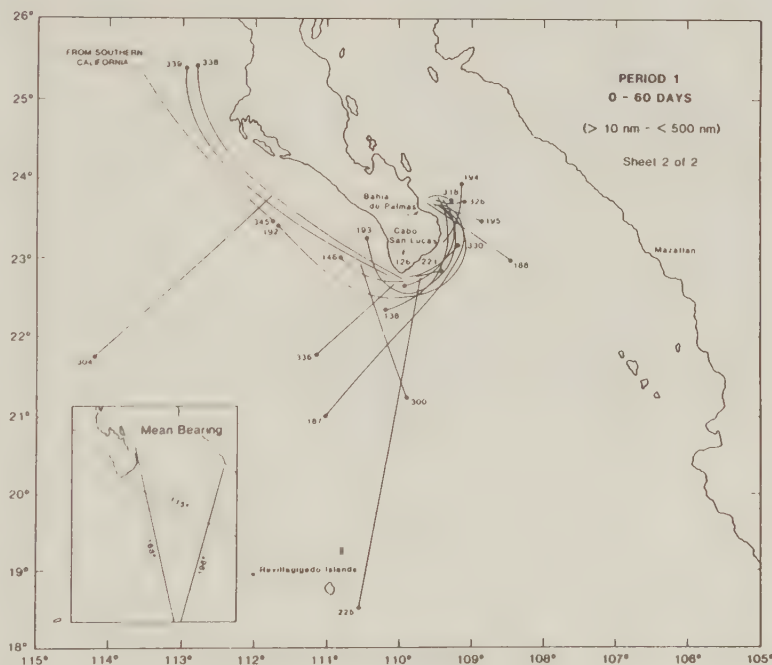
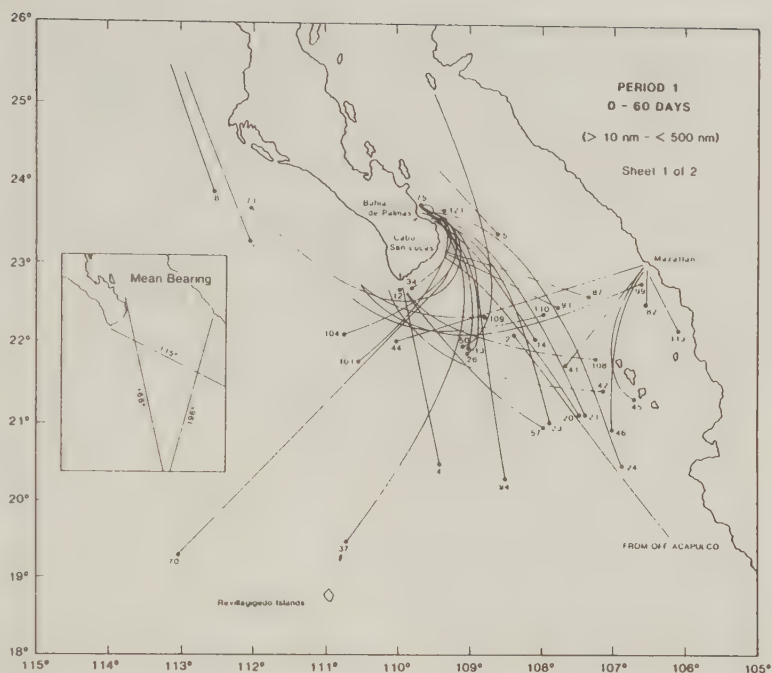
Figure 4.—Comparison of angler-estimated weights of striped marlin at tagging with weight at recovery, by release time and weight at recovery.

Figure 6.—Tag and recapture locations off Baja California Sur, Gulf of California, Mazatlán, and Acapulco for striped marlin released 0-60 days. Dot indicates tagging location. Line does not indicate migratory path. Mean bearing ($^{\circ}$ True) of recapture points to tagging location are shown.

tribution, which it is not. Striped marlin are tagged in an area as they migrate through it at various rates and directions. Numbers on the migration lines in Figures 6-10 indicate the NMFS Southwest Fisheries Center recovery number (Table 2).

For recoveries 0-60 days after tagging (Figure 6a, b) the mean bearing in degrees (True) from the location of tagging to area of recovery was for location of tagging off Cabo San Lucas, 115° , Mazatlán, 196° , and Bahía de Palmas, 168° . Although the mean bearing of tag recoveries is south to southeast from the southern tip of Baja California, several recoveries were made off and northwest of Magdalena Bay, indicating movement northwestward toward southern California, of striped marlin tagged about the southern tip of Baja California. Three recoveries from tagging off southern California, recovered within 60 days of release, were from recaptures of two striped marlin south of Magdalena Bay and one in the Bahía de Palmas area.

From 61 to 120 days after release (Fig. 7), most recoveries of striped marlin tagged near Cabo San Lucas and Bahía de Palmas were made to the south and southwest of Cabo San Lucas, generally in an area southwest of those recoveries observed with 60 days of release. Mean bearing for locations of tagging in relation to recovery points were for Cabo San Lucas, 182° , Mazatlán, 243° , and Bahía de Palmas, 201° . Some evidence of migration from the Bahía de Palmas/Cabo San Lucas area around the tip of Baja California was evidenced by four recoveries made south of Magdalena Bay. During the 61 to 120 day period after release two recoveries were made south of Magdalena Bay for striped marlin tagged off southern California.



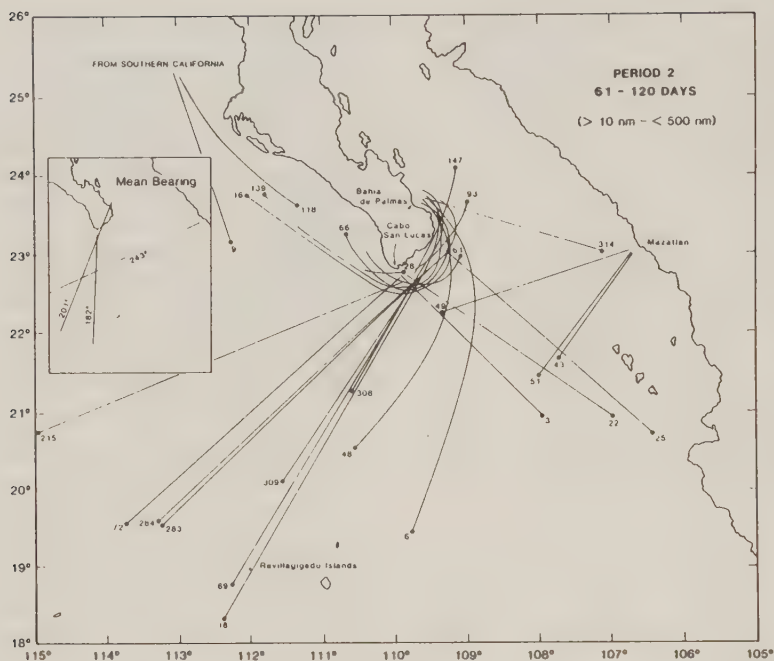


Figure 7.—Tag and recapture location for striped marlin having a release time of 61-120 days. Dot indicates tagging location. Mean bearing ($^{\circ}$ True) of recapture points to tagging location are shown.

The third time period (121-240 days after release) (Fig. 8) includes the mid-year (180 days) time of release. In considering an annual migration pattern, the 180-day time period could be important as it marks the time the fish might reach its most distant point from the tagging location. The mean bearing direction of recovery points in relation to tagging locations about the tip of Baja California again was shifted to the southwest. Mean bearing directions from tagging off Cabo San Lucas was 212° and Bahia de Palmas 196° . Five striped marlin were recovered northwest of Cabo San Lucas, between Cabo San Lucas and Magdalena Bay. The majority of recoveries were further southwest than those observed for the 61-120 day period.

Recoveries for release times of 241 days-1 year and for 1-2 years (Fig. 9a, b) were in the same area as those observed for the first two time periods. Recoveries of striped marlin tagged off southern California are given in Figure 10 and show a southern migration from the summer and early fall fishery. For recoveries of striped marlin tagged off southern California the mean bearing of recoveries 0-60 days was 153° . For the 61-120 days release time the recovery locations were 161° .

Rates of Migration

The average migration rate in nautical miles per day (n.mi./day) away from the location of tagging was calculated for the same time-at-large periods 0-60 days,

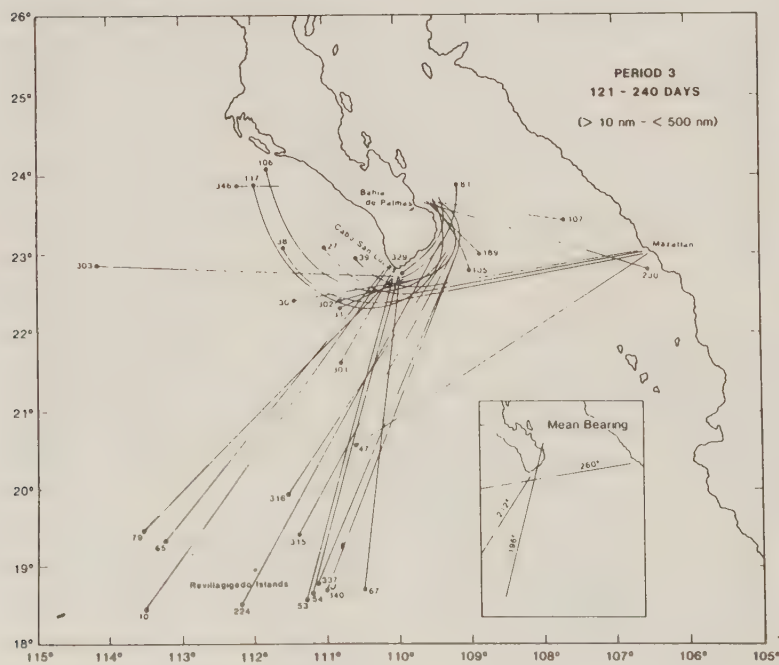


Figure 8.—Tag and recapture locations for striped marlin having a release time of 121-240 days. Dot indicates tagging location. Mean bearing ($^{\circ}$ True) of recapture points to tagging location are shown.

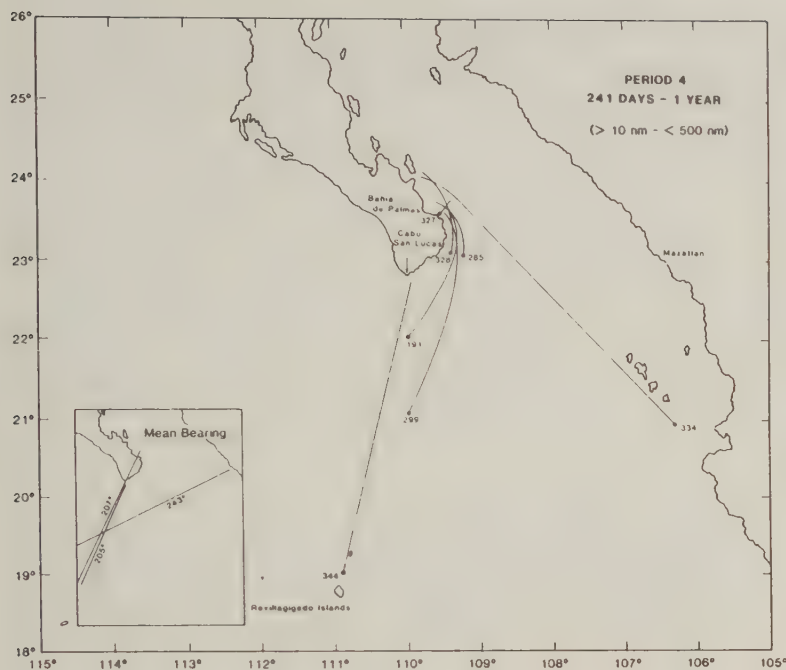


Figure 9.—Tag and recapture locations for striped marlin having a release time of 241-365 days and 1-2 years. Dot indicates tagging location. Mean bearing ($^{\circ}$ True) of recapture points to tagging location for both charts is shown on the Period 5 chart.

61-120 days, 121-240 days, 241 days-1 year, 1-2 years, and 2-3 years using data derived from time and distance from the tagging point to the recovery point. Table 6 gives the high and low migration rates observed in n.mi./day by tagging area and time period. The greatest observed migration rate for any striped marlin recovered was 31.5 n.mi./day; the fish was recovered after 80 days. The mean migration rate for all recoveries with time/distance data available was 1.6 n.mi./day.

For the first 120 days of release time, the average rate of migration about the southern tip of Baja California is much lower than the average rate of migration observed for fish tagged off southern California. Recoveries from southern California tagging recovered to the southeast or south averaged 13.3 n.mi./day. Recoveries from tagging in other areas distant from Baja California indicate that one recovery from Acapulco migrated northwest at a rate of 8.6 n.mi./day and one from Guaymas moved south at a rate of 8.3 n.mi./day.

I was most interested in the data obtained from recoveries within the first three time-at-large periods (0-60, 61-120, and 121-240 days) because these data may better define the average migration rate of striped marlin away from the major areas of tagging during the first half year of release. The average move-

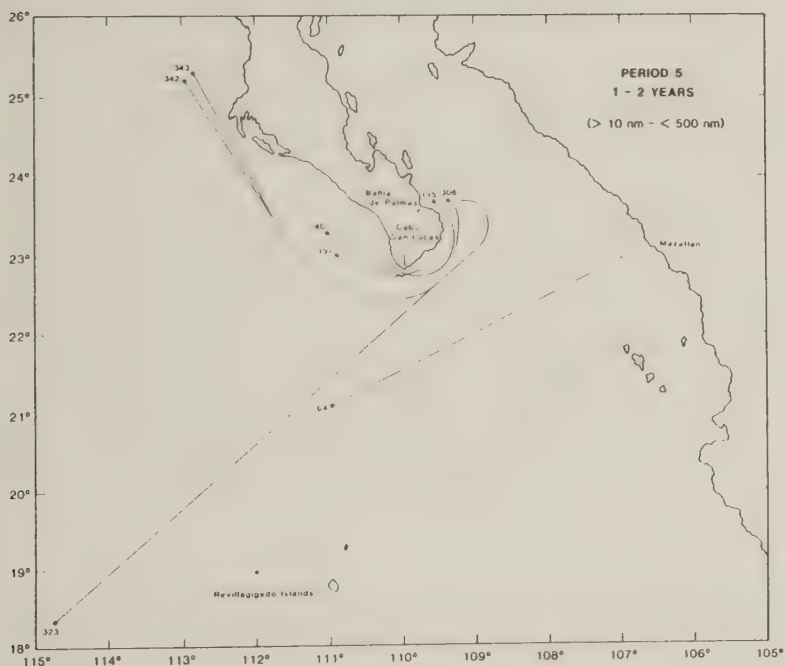


Table 6.—High and low migration rates (n.mi./day) by tagging area and time period.

Period	High/low in n.mi./day			
	S. Calif.	Baja Calif.	Sur	Mazatlán
0-60 days	25 7/9 5	31 2/0 42		8 3/2 5
61-120 days	31 5/5 6	26 0 0 59		2 3/1 4
121-240 days	None	6 2/0 28		1 7/1 1
241-365 days	None	0 8/0 03		None
1-2 years	10 0 9	1 0/0 5		10 0/1
2-3 years	None	10 0 0 1		None

ment in n.mi./day for the first three time periods was determined; then each rate was multiplied by the mean number of days within each time period in relation to zero day or date of tagging, to obtain the estimated average distance of migration per period of time-at-large. Average movement (n.mi./day) away from the tagging location for the three major areas of tagging and by time periods is given in Table 7.

A migration rate (n.mi./day) difference is evident between tagging periods in the two areas about the tip of Baja California Sur (Cabo San Lucas tip area and offshore Bahia de Palmas). I examined time and distance data for recovered marlin for differences in migration rates (n.mi./day) between these areas during the first 60 days of release time. For the Cabo San Lucas area during the winter months of November through March, the average migration rate for 13 recaptures was 4.45 n.mi./day. During the spring and early summer months of April through June, the average migration rate for 5 recaptures was 5.18 n.mi./day. For the Bahia de Palmas area, only one sample was available during the winter months of November through March. Twenty-seven recoveries were available from April through June. The average migration rate was 2.53 n.mi./day.

The average migration rate for the first 60 days for the eastern tip area (Bahia de Palmas) for both time periods combined (November-March, April-June) was 2.54 n.mi./day; off the southern tip area (Cabo San Lucas) for both time periods the rate was 4.6 n.mi./day. Therefore, striped marlin appear to be moving at about twice the rate in the southern tip area (Cabo San Lucas).

The average rate of migration from the southern tip of Baja California Sur peninsula decreases in the third time period from the date of tagging. The average migration rate for the first 60 days of release time was 4.2 n.mi./day, for 61-120 days release time the rate was 4.3 n.mi./day, and for 121-240 days the rate was 1.4 n.mi./day. For the nearby area of Mazatlán some decrease in average nautical miles per day was also evident; however, the average migration rate was about half that observed off the Baja peninsula. For 0-60 days of release time

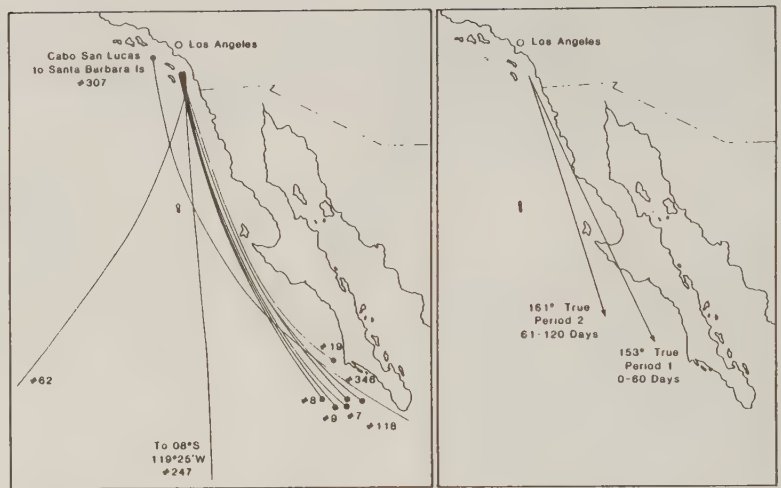


Figure 10.—Tag and recapture locations for marlin tagged off southern California. Numbers indicate month of tagging and number of days between tagging and recapture. Dot indicates recapture location and origin of line indicated tagging location. Line does not indicate migratory path. Mean bearings (°True) of recapture points to tagging locations are shown for recaptures for 0-60 days and 61-120 days.

Table 7.—Average movement away from the tagging location in nautical miles per day for each area, by time periods¹.

Area	Period	(Midpoint time in days)	No. in samples	Average n.mi./day	Period midpoint (n.mi.)
Baja, California Sur, Mex.	0-60 days	(30)	49	4.2	126
	61-120 days	(91)	23	4.3	391
	121-240 days	(181)	28	1.4	253
	241-365 days	(303)	7	0.4	121
	1-2 years	(547)	7	0.3	52
	2-3 years	(912)	1	0.01	9.1
Southern California, U.S.A.	0-60 days	(30)	6	11.3	339
	61-120 days	(91)	2	16.0	1,456
	121-240 days	(181)	1	11.7	2,117
	241-365 days	(303)	1	0.2	61
	1-2 years	(547)	1	0.1	55
	2-3 years	(912)	0		
Mazatlán, Mexico	0-60 days	(30)	9	1.8	54
	61-120 days	(91)	3	1.9	173
	121-240 days	(181)	1	1.3	235
	241-365 days	(303)	0		
	1-2 years	(547)	1	0.6	328
	2-3 years	(912)	0		

¹Recaptures from Acapulco (1) and Guaymas (1) averaged 8.64 and 8.26 n.mi. per day.

the rate was 1.9 n.mi./day, for 61-120 days the rate was 1.4 n.mi./day, and for 121-240 days the rate was also 1.4 n.mi./day.

A scatter diagram (Fig. 11) compares recovery points in nautical miles from point of tagging and release to elapsed

time in days from release for recoveries made within the first 240 days of release time from tagging off Baja California Sur. For marlin recovered more than 240 days after release about the Baja California Sur peninsula, the average distance from the tagging point to the recovery

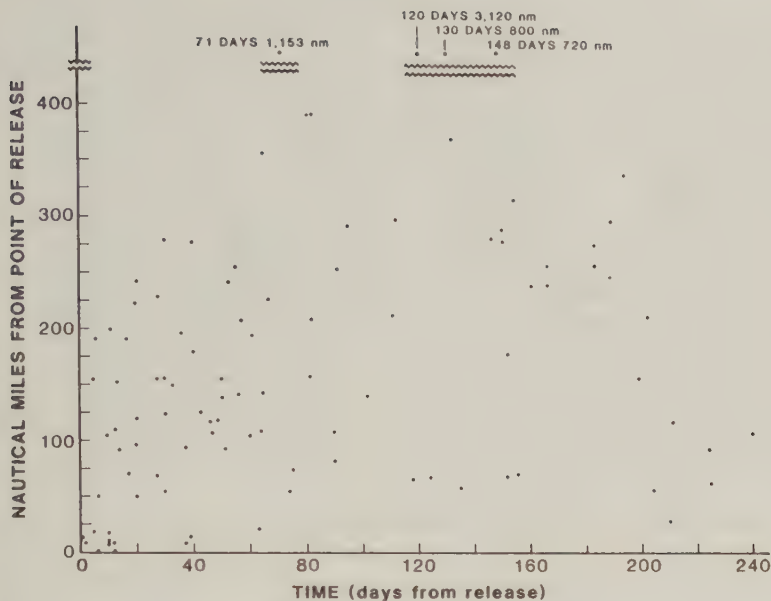


Figure 11.—Scatter diagram for first 240 days of release time for striped marlin tagged about Baja California Sur.

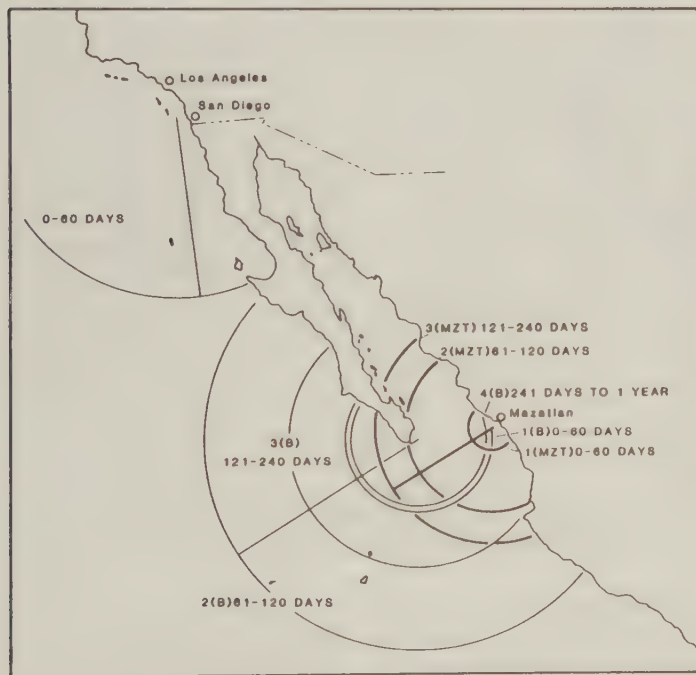


Figure 12.—Midpoint migration distances for time periods, tagging to recapture, 0-60 days, 61-120 days, and 121-240 days.

point was, for 241 days-1 year, 119 n.mi. (high, 207 n.mi., low, 12 n.mi.); for the 1-2 year period, 172 n.mi. (high, 410 n.mi., low, 20 n.mi.); and 5 n.mi. for the single recovery made 2-3 years after tagging.

Arcs showing average mileage limits for four time periods (0-60, 61-120, 121-240 and 241-360 days) for Baja California Sur recoveries were plotted (Fig. 12), using the average distance traveled from tagging to recovery per day by time period (average n.mi. per day times the midpoint for each time period).

Results would indicate a more rapid movement away from the southern tip of Baja California for marlin tagged during the late spring and early summer and during the 0-120 day period than for the following 121-240 day period. Long-term recoveries of one or more years were made in the area from Cabo San Lucas to the Revillagigedo Islands indicating that the striped marlin either remained in the area, or returned to it.

Discussion

Factors Related to and Affecting Tagging and Recovery

Tagging of large pelagics such as billfish cannot be done in large numbers, unlike with the smaller pelagics such as tuna. Also, it is difficult to obtain sufficient numbers of billfish to tag and release other than in areas having a productive rod-and-reel recreational fishery. In attempting to determine the general migrating pattern of billfish, data collected in other biological, physical oceanography, and catch analysis studies may be useful in developing a hypothesis to describe a migration pattern.

For a more ideal program to better define seasonal migration patterns, as an aid in determining stock boundaries, tagging effort should be distributed throughout the range of the species. For the migration patterns of striped marlin, tagging should be conducted in the northeast and southwest Pacific, central north Pacific, off Ecuador and around Galapagos Island, and in an area about 400 n.mi. west of Peru. The tagging effort reported here is from one portion of the striped marlin's distributional range—the northeast Pacific.

Tag Recoveries in the Eastern Pacific in Relation to the Geographical Distribution of the Longline Fishing Effort

The amount of fishing effort varies in the geographical areas fished by commercial longline, and these changes may affect the number of recoveries and recovery location. Data describing the catch and effort patterns for black marlin by the Japanese longline fishery operating off Queensland, Australia, have been useful in estimating migration patterns for black marlin in the southwest Pacific (Squire and Nielsen, 1983). Longline catch and effort data covering all the major oceans are published annually by the Research Department of the Japan Fisheries Agency, and these data are grouped by 5° longitude by 5° latitude areas and include results for striped marlin fishing.

From 1965 to 1975, striped marlin catch rates for the Japanese longline fishery in many areas of the northeast Pacific averaged 2.1 to 5.1 or more striped marlin per 1,000 hooks effective hooking effort (Suzuki and Honma¹); maximum catch rates in the Pacific Ocean were recorded near the tagging area off the Baja California peninsula. Figure 13 outlines for 1956-70 (from Joseph et al., 1974) the average level of Japanese longline striped marlin catch per thousand hooks fished in the eastern Pacific. The effectiveness index (E) of the effort on striped marlin (effective hooks/nominal hooks) has exceeded 1.0 in the eastern Pacific since 1964 indicating "targeting" on striped marlin resources (Suzuki and Honma¹).

Figure 14 illustrates the distribution of Japanese longline effort in the eastern Pacific at intervals of 5 years during which the tagging was conducted. Hook effort is distributed at levels of 1-2 million or more hooks per year per 5° longitude by 5° latitude area south and west of the tagging area in the equatorial area from about lat. 10°N to lat. 15°S. High

¹Suzuki, Z., and Misao Honma. 1977. Stock assessment of billfishes in the Pacific. Billfish stock assessment workshop, Honolulu, HI, 5-16 December 1977. Unpubl. working pap., 129 p.

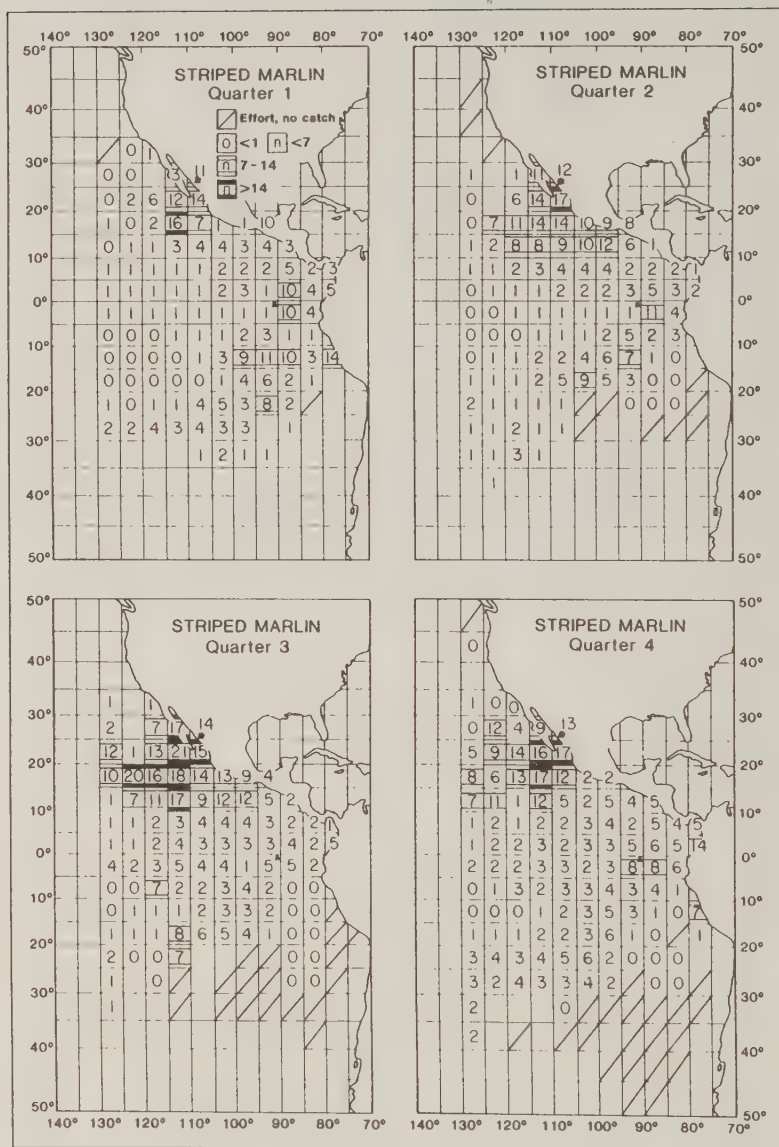


Figure 13.—Average number of striped marlin caught per 1,000 hooks by Japanese longline vessels in the eastern Pacific by quarters, 1956-70 and by 5° areas (from Joseph et al., 1974).

(1-2 million hooks) effort levels have been recorded 1,200 n.mi. southwest to 1,500 n.mi. west of the tagging area. In addition to the high hook effort near the area of tagging, these other areas of high effort provide possible recovery points

for striped marlin that migrate toward more distant waters.

Relationship of Tagging Results to Spawning

Presumably striped marlin spawn be-

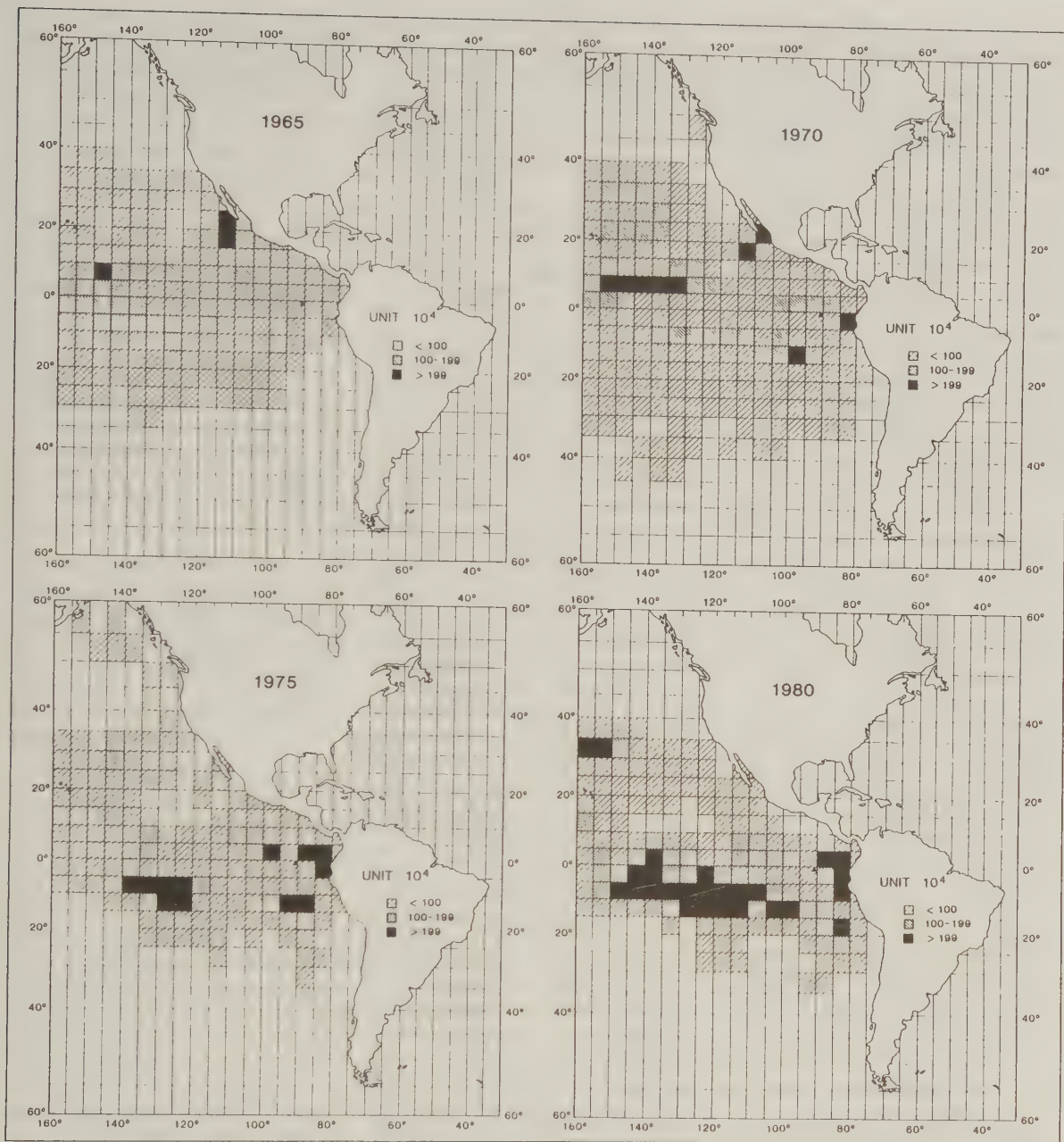


Figure 14.—Distribution of estimated total fishing effort in hook number for Japanese longline operations in the eastern Pacific.

tween June and October in the offshore areas of the northeast Pacific, south and southwest of Cabo San Lucas in the area of the Revillagigedo Islands (Joseph et al., 1974; Shoki²). Maturity is reached at

about 160 cm (eye-fork length) based on gonad indices (Kume and Joseph, 1969).

²Shoki, G. A., Manzanillo, Mex., 1965. Personal commun.

Japanese longline data for 1967 through 1975 (Suzuki and Honma¹) indicates that in the northeast Pacific (10° × 130°W) the greatest numbers of fish were caught in the 160-170 cm eye-fork length range.

Longline records taken in 1983-84 for striped marlin caught by joint-venture operations in the area about Baja California indicate the maximum number of fish in the 165-170 cm eye-fork length range. Both sets of data show a large catch under the 160-165 cm length range; therefore, the population of striped marlin in the reported spawning area southwest of Baja California would appear to be composed of a mixture of immature and mature fish.

Off Mazatlán, tagging was conducted primarily during late winter and spring months, before the predicted spawning in the northeast Pacific. Also, maximum tagging effort was conducted around the tip of Baja California Sur, in late spring and early summer before and at the beginning of the predicted spawning in the northeast Pacific. Developing gonads have been noted about the tip of Baja California Sur in June and July (J. Squire, personal observ.). However, they were not approaching the high gonad index levels of near-spawning as observed several hundred miles to the south or southwest from samples provided by Japanese longline vessels.

Tagging off southern California was done in the late summer and early fall during the predicted spawning period in the area southwest of the tip of the Baja California peninsula. Sampling of striped marlin off southern California in summer and early fall showed little gonad development (gonad indices <1.0) (Eldridge and Wares, 1974). Observations of gonad development, suggest that possibly half of the tagging of striped marlin about the southern tip of Baja California may be on the immature or prespawning segment of the population. The prespawners move offshore south and southwest of Cabo San Lucas toward a spawning or feeding area.

Physical Environment Relative to Migration

Hanamoto (1974), describing longline fishing conditions in the "target" areas off Mexico, noted the movement of the fishery for striped marlin in relation to a shift in thermocline depth. He reported that the pattern of expansion and contraction of the shallow-water thermocline area of about 30.5 m (100 feet) in depth

along Mexico's mainland and Baja California coast coincided with the pattern of seasonal expansion and contraction of good fishing grounds. Figure 15 is a composite of illustrations by Hanamoto (1974) which give the monthly distribution of mean relative abundance of striped marlin for 1966-70 and the monthly thermocline topography of the northeastern tropical Pacific.

Effects of Tagging and Hooking Mortality

Mortality of striped marlin as a result of the tagging process is not known. All marlin tagged were subjected to varying amounts of sublethal stress from hooking before they were tagged. Stress from hooking may not result in immediate mortality in most cases but may, in some cases, reduce the ability of the animal to cope with routine stress of the environment, and may ultimately result in an increased mortality rate (Wydoski, 1977). Hooking mortality studies on anadromous and freshwater species indicate a wide range of mortality levels, ranging from 10 percent to about 25 percent. The levels were related to the type of hooks and bait used in fishing. Hooking mortality plus natural mortality may result in a lower survival rate for tagged striped marlin.

No tag returns have been obtained for fish >3 years at large. This may be due to increased mortality due to hooking, tag loss, and the fact that a relatively small number of tags (average number tagged, 668/year) is being diluted by a large population of striped marlin (Bartoo and Ueyanagi, 1980). In comparison, Mather et al. (1974) reports that for the tagging in the western north Atlantic (with tags similar to those used in the Pacific) of 2,039 white marlin, *Tetrapturus albidus*, a species similar to striped marlin, and 216 tagged blue marlin, *Makaira nigricans*, 70 white marlin and one blue marlin were recovered. The recovery rates were 3.4 percent for white marlin and 0.4 percent for blue marlin. The population estimate for white marlin in the northwest Atlantic is considerably smaller than the population estimate for striped marlin in the Pacific (Shomura, 1980; Zuboy³). Higher recovery rates than those for striped marlin in the northeast Pacific,

such as those observed for black marlin in the southwest Pacific (2.3 percent) and for white marlin in the Atlantic (3.4 percent) may be related to lower tag dilution rate, relative to population size.

Estimates of the Central Tendency of Migration

A tentative hypothesis can be developed describing the central tendency of migration direction and rate for striped marlin in the northeast Pacific. Using information derived from the graphic plots of tag and recovery points, the migration direction and rate analysis, movements of high CPUE areas in the commercial longline fishery over time, the geographical distribution of longline fishery effort in the total eastern Pacific, and the spawning behavior exhibited in the northeast Pacific, I suggest the following:

- 1) In the northeast Pacific areas of high CPUE, striped marlin move south or southwest from the tagging area in the summer and early fall and then move northward toward the Baja California peninsula in the winter and spring seasons. Tagging results parallel the seasonal catch distribution of the longline fleet.

- 2) The seasonal shift of thermocline depth in relation to catch distribution changes are similar to the seasonal geographical changes observed in longline CPUE rates.

- 3) Movement of striped marlin from an area of low gonad indices or a non-spawning area about the tip of Baja California to an area of high gonad indices and reported spawning south and southwest gives support to the results of tagging which show similar movements.

- 4) Recovery data indicate a predominate movement south from tagging off southern California, and the data indicate that some marlin from about the tip of Baja California Sur migrate northwest to off southern California.

- 5) Because few (5 or 3.2 percent) of the total recovered marlin were caught at

³Zuboy, J. R. 1977. Atlantic billfish stock assessment. Billfish Technical Workshop, Honolulu, HI, 5-19 December 1977. Working pap. QP-2, 36 p., unpubl.

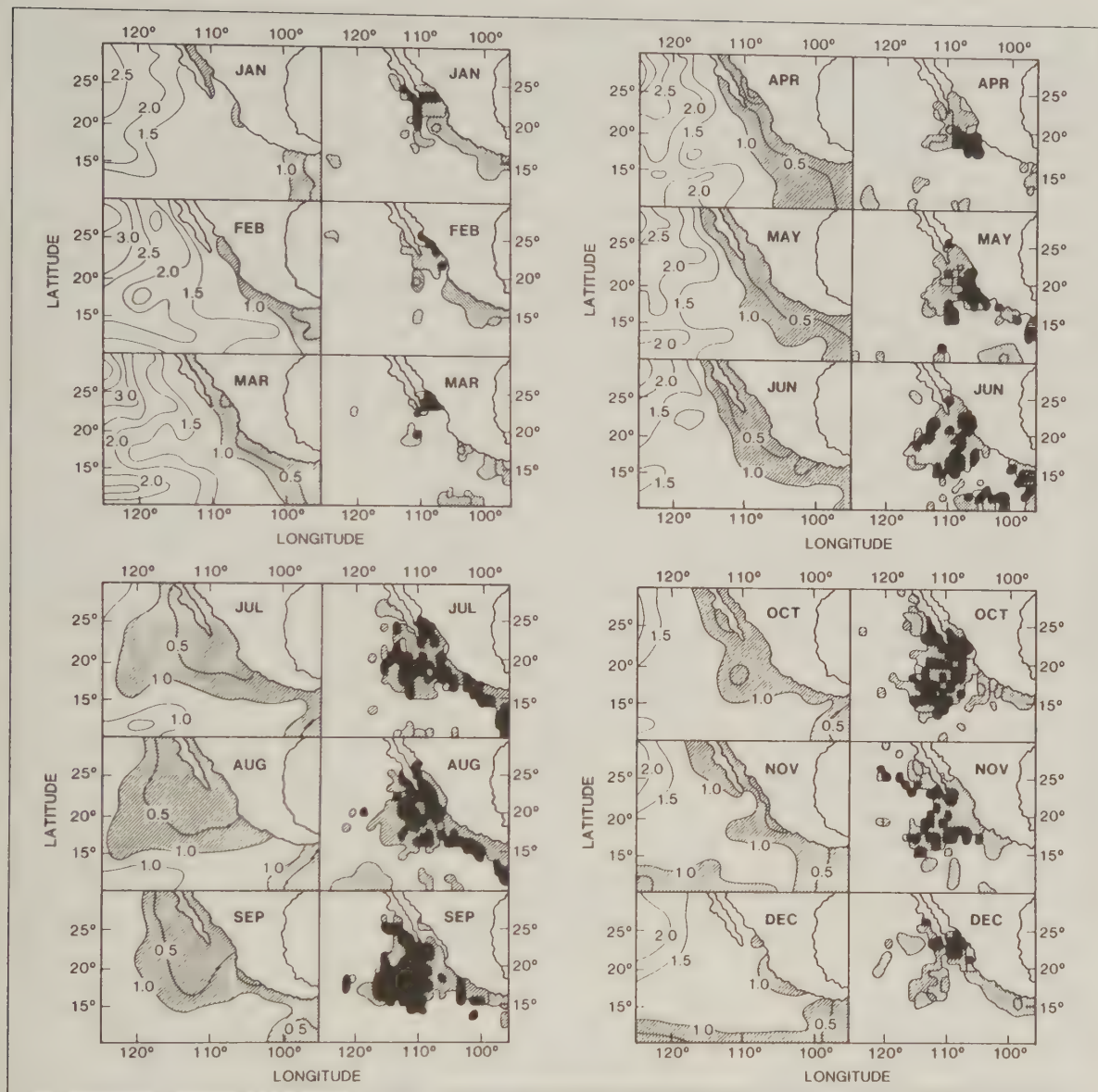


Figure 15. —Monthly distribution of mean relative abundance of striped marlin and monthly thermocline topography for fishing areas off Mexico, 1966-70. Numbers on the contour line represent the depth to the top of the thermocline in hundreds of feet. Areas of relative abundance are: high abundance (>1.5 percent), dark areas; medium abundance (1.4 to 0.5 percent), hatched areas; low abundance (>0.5 percent), stippled areas (from Hanamoto, 1974).

a distance greater than 800 n.mi. from the point of tagging, striped marlin cannot be considered short-term distant-water migrators in the Pacific, like

bluefin tuna, *Thunnus thynnus*, and albacore, *Thunnus alalunga*.

The migration of striped marlin in the

northeastern Pacific area of tagging and of the commercial longline fishery can be hypothesized from the results of tagging (Fig. 16). The tagging results indicate

that the migratory rates and patterns of striped marlin are highly variable. There is, however, a central tendency of movement of tagged striped marlin which is similar to the shifts in CPUE; the movement of tagged fish is also patterned by biological and environmental factors that occur in the tagging and fishing area.

The recreational rod-and-reel fishery that has tagged and released striped marlin off Baja California is fishing on the same population as the commercial longline fleet operating about the tip of Baja California, as the recreational fishery and the commercial longline fishery and the recreational fishery catch-per-unit-effort (CPUE) exhibited a coefficient of correlation of $r_2 = 0.82$ (Squire, 1982). The relation of migratory patterns of striped marlin tagged in the northeast Pacific to striped marlin resources common to other geographical areas is unclear. However, the fluctuations and the downward trend of the commercial longline catch rate for areas about the southern tip of Baja California (lat. $20^\circ\text{N} \times \text{long. } 109^\circ\text{W}$ and 105°W) appears to be similar to other areas in the eastern Pacific (Fig. 17). Throughout most of the remaining eastern Pacific striped marlin is not a target species for the longline fishery, and catches are incidental to catches of tuna and other species of billfish. The similarity of catch rate trends (Fig. 17) indicate that there is a relationship between the population of striped marlin that is being subjected to targeting off Mexico (25-28 percent of the eastern Pacific catch) and to striped marlin common to other areas of the eastern Pacific.

Relation of the Findings to Management

One of the primary purposes of this tagging program is to provide data for management decisions relative to the resource stock structure of striped marlin. The stock structure of striped marlin is not fully understood; also, if any striped marlin substocks exist they have not yet been identified.

Three possible stock structure hypotheses have been proposed for striped marlin in the Pacific. At the 1977 Billfish Stock Assessment Workshop in Honolulu, Hawaii, Suzuki and Honma¹ suggested a northwest, southwest, and east-

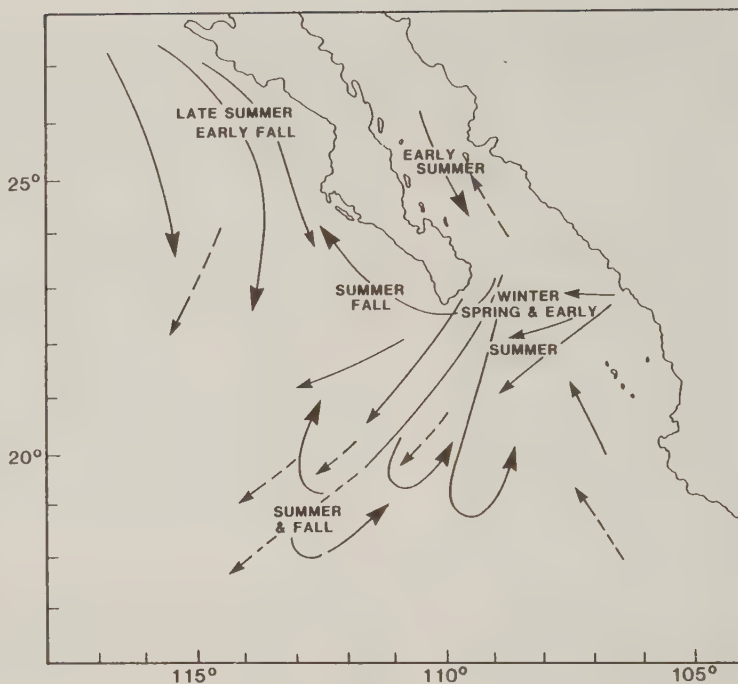


Figure 16.—Hypothetical striped marlin migration patterns for the northeast Pacific.

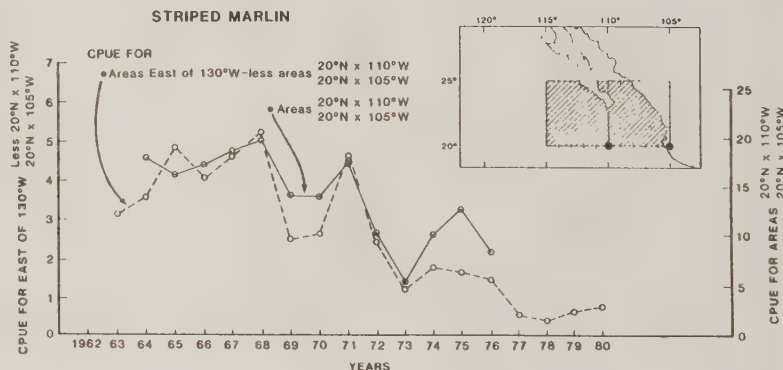


Figure 17.—Fluctuations in the Japanese longline CPUE for two 5° areas off Baja California, and the CPUE for the eastern Pacific (E of long. 130°W) less the two 5° areas.

ern Pacific stock division, based on biological and catch distribution evidence. The two other stock structure hypotheses which were believed most tenable at that time (Shomura, 1980) were:

1) A single-unit stock in the Pacific. This hypothesis is supported by the continuous distribution of striped marlin in a horseshoe-shaped pattern. 2) A two-stock structure, with the stocks separated

roughly at the equator into North Pacific and South Pacific stocks and with some intermixing in the eastern Pacific. The two-stock hypothesis is supported by morphometric differences between adults from the north and south regions of the western Pacific (Kamimura and Honma, 1958) and perhaps also in the eastern Pacific (Howard and Ueyanagi, 1965). Kamimura and Honma (1958) also noted that there is a zone of low longline catch rates along the equator in the central and western Pacific. Larval distribution suggests two centers of spawning, one in the northwest and one in the southwest Pacific. Gonad index data (Kume and Joseph, 1969) suggest that spawning occurs throughout the eastern tropical Pacific, the supposed region of stock mixing.

The relationship of striped marlin migration observed patterns from tagging in the northeast Pacific to striped marlin inhabiting other areas of the Pacific is unclear. Relatively short migrations were common in the northeast Pacific; few recaptures in distant areas would indicate a minimum of mixing. Long-range movements over time are possible; however, only 3.2 percent of the recoveries were at a distance of greater than 800 n.mi. from tagging. Nonetheless, if a high percentage of striped marlin migrated considerable distances away from the tagging area, they would still be subject to incidental recapture since the commercial longline fishery operates over a large area at considerable distances from the tagging area.

The long-term interchange rate of the population found in the northeast Pacific with the population of the northwest and southwest Pacific area is unclear. No recaptures have been made in these areas, although a small percentage of the recaptured fish was headed in those directions, which indicates that some population interchange could be expected over time. Therefore, defining the various populations of these areas as "unit stocks" as required for stock assessment methods (Cushing, 1970) may be academic in the case of striped marlin.

The results of this migration study, when combined with other information developed from studies of striped marlin biology, fishery dynamics, and catch dis-

tribution, would indicate that the northeastern Pacific resource of striped marlin, though not meeting the unit stock criteria for management purposes as defined by Cushing (1970), could be considered a manageable resource unit of a greater Pacific resource to the extent that this area off Mexico contributes about 25-28 percent of the total eastern Pacific catch of striped marlin and 14 percent of the total Pacific catch (1962-80). If management regulations were adopted for the northeast Pacific unit it would have an impact on the status of the striped marlin resource and the associated recreational and commercial fisheries (Squire, 1982). However, management of the striped marlin resource in the Pacific on a resource unit basis would be required to include all high catch rate and target fishing areas, and would likely be part of a comprehensive international management plan for billfish and tuna.

Acknowledgments

The cooperation of the marine anglers who caught, tagged, and released striped marlin made this study possible. Their support and willingness to participate and the support of such organizations as the International Game Fish Association, National Coalition of Marine Conservation, and the major billfish clubs of southern California, enable us to carry out this work. In particular, our appreciation goes to Horace Witherspoon, Herb Kameon, and Ed Martin, for without their assistance tagging in both southern California and Baja California would have been much less successful. In Baja California Sur, where most of the striped marlin were tagged, special thanks go to Eugene Walters (now deceased), operators of Rancho Buena Vista⁴, S.A., long-time supporters of the tagging program and other scientific studies in the Baja area, and to the current staff of Rancho Buena Vista, Ted Bonney, Mark Walters, and the fishing captains, and to the captain tagging and releasing the most striped marlin in the eastern Pacific, Jesus Ariza Ruiz. Others in the Baja California Sur area have given outstanding

support: These include Jorge Excudero, Bob Van Wormer, Bud Parr, and most of the charter boat operators about the tip of Baja. Without the cooperation of these individuals, and the U.S. sportfishing boats that frequently fish and tag in the Baja area, in addition to tagging off southern California, increased knowledge of the oceanic migration patterns of billfish would not be possible.

Recaptures of tagged fish are just as important as tagging, and we wish to convey our appreciation to the Japanese and Korean commercial longline fleet captains and crews and to the marine anglers who recaptured tagged marlin and returned the tags. Guillermo Adachi of Manzanillo and Mario Comparan of Ensenada, Mex., have been of assistance through contacts with the Japanese longline operations off Mexico. The Japan Fisheries Agency, Far Seas Fishery Research Laboratory, Shimizu, Japan, has also been instrumental in returning tags from striped marlin recaptures by the Japanese fleet, and these important efforts are appreciated.

Literature Cited

- Anonymous. (1962-80.) Annual report(s) of effort and catch statistics by area on Japanese tuna longline fishery. Rec. Div., Fish. Agency Jpn., var. pagin.
- Bartoo, W., and S. Ueyanagi. 1980. Rapporteur's report - striped marlin, *Tetrapturus audax*. In Summ. Rep. Billfish Stock Assessment Workshop Pacific Resour. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC-5, p. 20-29.
- Cushing, D. H. 1970. Fisheries biology. Univ. Wisc. Press, Madison, 200 p.
- Eldridge, M. B., and P. G. Wares. 1974. Some biological observations of billfishes taken in the eastern Pacific Ocean, 1967-1970. In R. S. Shomura and F. Williams (editors), Proc. int. billfish symp. Kailua-Kona, Hawaii, 9-12 Aug. 1972. Part 2. Rev. Contrib. Pap. p. 89-101. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.
- Hanamoto, E. 1974. Fishery-oceanographic studies of striped marlin, *Tetrapturus audax*, in waters off Baja California. I. Fishing conditions in relation to the thermocline. In Kailua-Kona, Hawaii, 9-12 Aug. 1972. Part 2. Rev. Contrib. Pap., Proc. Int. Billfish Symp. p. 302-308. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.
- Howard, J. K., and S. Ueyanagi. 1965. Distribution and relative abundance of billfishes (Istiophoridae) of the Pacific Ocean. Univ. Miami Inst. Mar. Sci. Stud. Trop. Oceanogr. 2, 134 p.
- Joseph, J., W. L. Klawe, and C. J. Orange. 1974. A review of the longline fishery for billfishes in the eastern Pacific Ocean. In R. S. Shomura and F. Williams (editors), Proc. Int. Billfish Symp. Kailua-Kona,

⁴Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

- Hawaii, 9-12 Aug. 1972. Part 2. Rev. Contrib. Pap., p. 309-331. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.
- Kamimura, T., and M. Honma. 1958. A population study of the so-called makajiki (striped marlin) of both northern and southern hemispheres of the Pacific. I. Comparison of external characters. Rep. Nankai Reg. Fish. Res. Lab. 8:1-11 (in Jpn. with Engl. synop.).
- Kume, S., and J. Joseph. 1969. Size composition and sexual maturity of billfish caught by the Japanese longline fishery in the Pacific Ocean east of 130°W. Bull. Far Seas Fish Res. Lab. (Shimizu) 2:115-162 [in Engl.].
- Mather, F. J., III, J. M. Mason, Jr., and H. L. Clark. 1974. Migrations of white marlin and blue marlin in the western north Atlantic Ocean—tagging results since May, 1970. In R. S. Shomura and F. Williams (editors), Proc. Int. Billfish Symp. Kailua-Kona, Hawaii, 9-12 Aug. 1972. Part 2. Rev. Contrib. Pap., p. 211-225. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.
- Nakamura, I. 1974. Some aspects of the systematics and distribution of billfishes. In R. S. Shomura and F. Williams (editors), Proc. Int. Billfish Kailua-Kona, Hawaii, Aug. 1972. Part 2. Rev. Contrib. Pap., p. 45-53. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.
- Shomura, R. S. (editor). 1980. Summary report of the billfish stock assessment workshop Pacific resources. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC-5, 58 p.
- Squire, J. L. 1974. Migration patterns of Istiophoridae in the Pacific Ocean as determined by cooperative tagging programs. In R. S. Shomura and F. Williams (editors), Proc. Int. Billfish Symp. Kailua-Kona, Hawaii, 9-12 Aug. 1972. Part 2. Rev. Contrib. Pap., p. 226-237. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.
- _____. 1982. 1982 Billfish newsletter. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., La Jolla, Calif., 10 p.
- _____. 1986. 1986 Billfish newsletter. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., La Jolla, Calif., 11 p.
- Squire, J. L., Jr., and D. V. Nielsen. 1983. Results of a tagging program to determine migration rates and for black marlin, *Makaira indica* in the southwest Pacific Ocean. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-772, 19 p.
- Suda, A., and M. B. Schaefer. 1965. General review of the Japanese tuna longline fishery in the eastern Pacific Ocean 1956-1962. Bull. Int. Am. Trop. Tuna Comm. 9(6):1-462.
- Talbot, G. B., and P. G. Wares. 1975. Fishery for Pacific billfish of southern California and Mexico, 1903-69. Trans. Am. Fish. Soc. 104(1):1-12.
- Ueyanagi, S. 1974. A review of the world commercial fisheries for billfishes. In R. S. Shomura and F. Williams (editors), Proc. Int. Billfish Symp. Kailua-Kona, Hawaii, 9-12 Aug. 1972. Part 2. Rev. Contrib. Pap., p. 1-11. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-675.
- Wydoski, R. S. 1977. Relation of hooking mortality and sublethal hooking stress to quality fishery management. In R. A. Barnhart and T. D. Roelofs (editors), Proc. the Natl. Symp. Catch Release Fishing, Humboldt State Univ. Sept. 1977, p. 43-87. Calif. Coop. Fish Unit, Humboldt State Univ. Arcata, Calif.

Fishing Effort: Its Testing, Specification, and Internal Structure in Fisheries Economics and Management¹

DALE SQUIRES

*National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271,
La Jolla, California 92038*

Received October 22, 1984; revised April 7, 1986

The concept of fishing effort is central to fisheries economics and management. However, effort is an aggregate index of inputs which can be consistently formed only under the condition on production technology of homothetic separability of inputs. This paper develops the conditions under which effort can be consistently formed. It then provides the first empirical test for effort and jointness in inputs in a fishery by estimating a multiproduct function for the New England otter trawl fleet. After not rejecting input-output separability and rejecting nonjointness in inputs, the construction of a superlative index for effort is demonstrated through estimating a translog production function. The implications of effort's internal structure for fisheries management are then considered. © 1987 Academic Press, Inc.

1. INTRODUCTION

The concept of fishing effort is central to fisheries economics and management [2, 9, 28]. Much of fisheries management is centered upon regulating the level of effort [2, 28]. Practical management requires regulating one or more components of effort, which in turn requires empirical knowledge of effort's internal structure. Effort also plays a crucial role in the specification of both static and dynamic bioeconomic models [2, 9]. In this case, effort is typically part of a multistage optimization process [1]. In the first stage, factors of production such as capital, labor, and energy are (usually implicitly) optimally and efficiently combined to form a composite input index, effort. In the second stage, effort typically becomes an input in the fishery production function. The concept of effort has yet a third fundamental role in fisheries economics and management. Estimates of effort are commonly employed in conjunction with commercial fish landings to provide a measure of relative resource abundance through the catch per unit effort index (CPUE), to estimate fishing mortality, and to track trends in industry productivity and performance over time [10].

The concept of fishing effort is thus a fundamental component of bioeconomic models, public regulation, relative resource assessment, and productivity analysis of marine fishing industries. Yet, since effort is an aggregate index of the individual factors of production, these separate components of effort can only be consistently aggregated into a composite index under a fairly restrictive condition on the production technology, homothetic separability.

Bioeconomic models not only *a priori* assume a composite input, effort, but in multispecies fisheries, often assume a single production process. That is, the

¹The comments of Sam Pooley, Virgil Norton, Jim Kirkley, Dan Huppert, and two anonymous reviewers are gratefully acknowledged. Any remaining errors are the responsibility of the author. The results presented do not necessarily represent those of the National Marine Fisheries Service.

presumed fishery production technology requires all inputs to harvest all outputs, which is joint-in-inputs production. If the true harvesting technology is instead nonjoint-in-inputs (output independence), then a separate production function should be specified for each species or block of species (block independence). Moreover, when modeling or regulating only a select species, bioeconomic modelers and fishery managers typically make the opposite assumption, that production is nonjoint in inputs. In this case, it is assumed that separate production processes exist, and that each process can be separately regulated without affecting production from any other process.

Fishery economics and management thus invariably maintain hypotheses upon the production technology: the existence of a consistent aggregate input, fishing effort, and if the fishery is multispecies, either nonjoint or joint production. If these conditions on production technology do not hold, then misleading results might occur in analysis and management. For example, should the true multispecies harvesting technology be joint in inputs, then a single production process exists for all the species. A bioeconomic model may instead specify nonjoint-in-inputs production (a separate production function for the species of concern) and optimize the level of effort and catch for only one of the many possible species in the fishery. The optimized results will neglect the other species and any possible species transformations in harvesting. The results will further rely upon either the tenuous allocation of joint costs to a single product or determination of harvest costs of a single output while ignoring the joint costs (which are likely to be lower) [16]. Fishery managers will then be provided misrepresentative optimum levels of total catch, total effort, and resource availability. Public regulation based on this approach is likely to be disappointing and ineffective.

Alternatively, should the harvesting technology not be homothetically separable in inputs so that an effort index cannot be properly constructed, the bioeconomic procedure will provide inconsistent results for regulation. The levels of effort and costs will be inconsistent as the catch changes: different optimal and efficient input bundles may be associated with the same level of effort, or conversely, different effort levels may be associated with the same optimal input bundle. Public regulation attempting to regulate with these results is likely to obtain unexpected results.

The purpose of this paper is to explicitly address the commonly maintained hypotheses on production technology inherent in fisheries economics and management: homothetic input separability and jointness in inputs. Rather than rely upon the questionable existence of an aggregate production technology, the study is specified at the level of the firm. This paper first formally develops the relevant concepts and provides empirical tests. The paper next demonstrates the proper empirical construction of a consistent aggregate index for effort. The internal structure of effort is then examined and the implications for public regulation noted. These concepts are empirically demonstrated through a case study of the New England otter trawl industry with firm-level panel data.

2. THE EXISTENCE OF AGGREGATES

Consider a multiproduct firm producing M products from N inputs. The set of efficient input-output combinations may be described by the firm's transformation frontier. If one output is singled out as a numeraire commodity, say Y_M , then the

asymmetric transformation frontier may be defined as the maximum amount of Y_M which can be produced given the amount of the other $M - 1$ outputs, Y' , and N inputs X' : $Y_M = F(Y_1, Y_2, \dots, Y_{M-1}, X_1, X_2, \dots, X_N)$.

The existence of effort (E) becomes a question of determining the conditions on the production technology under which an aggregate input index can be formed. That is, when can the transformation frontier be collapsed to: $Y_M = F(Y', E)$, where $E = f(X_1, X_2, \dots, X_N)$ and f is a consistent aggregator function? In this case, the optimal amount of effort is first determined by solving the optimization problem $E = f(X')$ and then in the second stage of production, Y_M is optimized given Y' and E .

Separability is the relevant property of technology which allows aggregation of individual inputs into the aggregate variable fishing effort. Intuitively, the aggregate $E = f(X_1, X_2, \dots, X_N)$ can be formed if it is possible to meaningfully rank alternative levels of effort (represented by isoquants) without knowing the levels and mixes of species harvested. Comparisons of various levels and combinations of the inputs comprising effort, i.e., comparing the isoquants, can be made independently of Y' . Thus if a fishing firm harvests more cod and less yellowtail flounder, the ranking of the input isoquants in effort is not affected, that is, the isoquants remain nested. Monotonicity still holds, since more inputs will generate at least as high a level of effort, and the isoquants radiate outward. If effort is not separable, then any attempt to construct E from X' will lead to an index for effort which varies with variations in quantities and mixes of outputs (effort isoquants twist around and might even intersect), and it is not possible to obtain a meaningful scalar measure for effort.

Several types of separability exist, but the generally relevant type for aggregation is weak separability.² Weak separability requires that the marginal rates of technical substitution (MRTS) between all pairs of variables in a particular group (such as effort) are independent of changes in the levels of variables not in that group (here, outputs). Strong separability is a more restrictive form of separability, and requires that the MRTS between variables of different groups be independent of the levels of variables in any other group. Strong separability implies weak separability, but the converse applies when only two subsets exist.

Separability can occur at various levels of aggregation. At the highest level, separability between inputs and outputs implies composite indices for both total catch and effort. Input-output separability implies that the marginal rates of substitution (transformation) between input (species) pairs are independent of the composition of catch (effort). In this case, F is additively separable in composite inputs and outputs: $g(Y', Y_M) - f(X') = 0$, where f and g are aggregator functions. An input-output separable harvesting technology implies that fishermen make their decisions on optimal species independently of their decisions on factor combinations. Fishermen select their species on the basis of expected relative species prices and prior knowledge subject to the technological constraints imposed by resource availability and weather conditions. Alternatively, changes in relative species prices do not affect production decisions on the optimal combinations of capital, labor, and fuel. The next relevant level of separability for the existence of

²Implicit separability also allows aggregation [6]. Hicks or Leontief separability further allow formation of aggregates, where prices or quantities move in fixed proportions over time; this condition is difficult to apply in cross-sectional or panel data sets.

effort is weak separability of all inputs, in which case F may be written: $Y_M = F(Y', f(X'))$.

While weak separability of the technology in all inputs is necessary and sufficient for the existence of the aggregate E , homotheticity is a necessary and sufficient condition for the validity of sequential optimization. Homotheticity insures expansion paths for the inputs comprising effort which are rays emanating from the origin. The within-group factor proportions are independent of the total level of effort. Homothetic separability of E exists if the production technology is weakly separable in X' and the aggregator function for effort, f , is linear homogenous [22]. The transformation frontier F is homothetically separable in inputs when $Y_M = F(Y', f(X'))$, where f is homogeneous degree one in X' . Homothetic separability ensures that consistent quantity and price indices exist, so that the product of the aggregate price and quantity indices of effort equals the total cost of the components of effort. Graphically, the set of all input isoquants comprising E , input expansion paths, and MRTSs between factors are fixed and independent of the particular combinations of outputs, and input expansion paths are rays from the origin with equally spaced and identically shaped isoquants. Separability between inputs and outputs and homogeneity of F is a more restrictive condition and implies the consistent formation of composite indices for both catch and effort.

Joint-in-inputs multiproduct production requires all inputs to produce all outputs, while nonjointness in inputs implies separate production functions for each output or sets of outputs. Lau shows that a transformation frontier $Y = F(Y', X')$ is nonjoint in inputs if there exist individual quasi-concave, nonnegative, monotonic functions $Y_i = f_i(X_{i1}, \dots, X_{iN})$, $i = 1, 2, \dots, M$, such that $F(Y', X') = \max \sum_i f_i(X_{i1}, \dots, X_{iN})$ and $\sum_i X_{ij} = X_j$, $j = 1, \dots, N$, and the inputs are so allocated amongst the processes that the product of no one process may be increased without decreasing the output of some one process. Production activities may therefore be consolidated, but there is not a technological trade-off between the output of one activity at the expense of another since it is possible to fully allocate the services of all inputs to each of the outputs. In contrast, a joint-in-inputs production technology implies some positive or negative external effect from one product on the production of other outputs. In the short-run, the jointness arises from either allocatable (quasi-fixed) factors or interdependent production processes, while in the long-run, only from the latter. Lau shows that input-output separability implies either jointness in inputs or individual production functions that are identical except for a scalar multiple, effectively implying only a single kind of output.

3. EMPIRICAL SPECIFICATION AND HYPOTHESIS TESTS

The general specification of the production technology and empirical tests for jointness in inputs and a consistent aggregate input index for effort are developed for an application to the New England otter trawl industry. This industry includes some of the world's most valuable fishing grounds. The most important species landed by value include cod, yellowtail and other flounders, haddock, redfish, and pollock. A typical fishing trip begins by steaming to the selected initial fishing grounds. The otter trawl net is released and dragged from the stern or side of the

vessel. After some time, the catch is hauled in, released onto the deck, and the cod, haddock, and pollock gutted, sorted, and packed in ice. After return to port, proceeds from the sale of the catch are distributed among the vessel, crew, captain and trip expenses by the lay or crew share system. The particular share system formula followed varies by port, and to a lesser extent, vessel. Moss and Terkla [26] and Wilson [34] provide further details of the industry and harvesting process.

These industry characteristics provide guidelines for modeling the firm's production technology. First and foremost, a multispecies fishery implies a multiproduct technology, which should include as outputs the most important species, cod, haddock, and yellowtail and other flounders. Second, during the time period of concern, 1980–1981, outputs can largely be regarded as freely variable and endogenously determined, so that the outputs are not restricted by regulation.³ Third, crew sizes are variable, although probably only within a range, and more so in larger vessels than smaller ones. Fourth, fishing vessels produce the vector of endogenous outputs from a vector of endogenous inputs, labor, fuel, and capital (vessel, engine, equipment, and gear).

Specification and estimation of the fishing firm's production technology by the multiproduct transformation frontier F provides one approach, but it is a difficult and limited one to empirically apply [18]. However, as is well known, the structure of technology can be examined either directly by the primal approach or indirectly by a dual formulation [8, 22]. Tests of separability, homotheticity, and joint-in-inputs production can therefore be readily applied with the dual procedure. Since both outputs and inputs are decision variables to firms, the multiproduct profit function is the preferred dual representation of technology. Moreover, the presence of well-defined auction markets, homogeneous product types, and minimal vertical and horizontal integration among a large number of firms assure exogenously determined product prices. The endogenously determined returns to labor (by the lay system) is given its proper economic and exogenous valuation by use of the opportunity cost of labor. Profits are therefore economic rather than accounting profits.

The issue of selecting a restricted or full static equilibrium specification of technology also arises. The lumpiness and long life of fishing vessels suggest a restricted model with capital as a fixed factor. Alternatively, a full static equilibrium model may be more suitable, since important used and new vessel markets, vessel leasings, and deliberate sinkings for insurance exist. Otter trawlers are also mobile and can easily switch to a gear, location, or targeted species other than those of the owners' original intentions. Perhaps most importantly, long-run investment decisions are likely to be made with expectations of a wide range of cyclical and stochastic fluctuations in resource abundance but a relatively constant spatial distribution of different species or stocks. Moreover, vessels of a certain size and design are required to fish in the stormy Northwest Atlantic and to reach fishing grounds. Squires [30] finds full static equilibrium to be the appropriate specification after application of Kulatilaka's [21] test.

³ Personal communication, Dr. Guy Marchesseault, Deputy Director, New England Fishery Management Council. Some industry observers, such as Dr. James Wilson, Chair of the Statistical and Scientific Committee of the Council, feel that even by 1980, *de facto* regulation was virtually absent. Moreover, even if limits on the catch of each trip were to some degree binding in 1980, the use of annual data suggest that as fishermen make more frequent and shorter fishing trips, outputs are still variable, but at the cost of technical inefficiency.

The multiproduct firm's profit function provides the maximum (economic) profit as a function of product and factor prices. The profit function H is derived from the firm's maximization problem. Subject to the transformation frontier F , assume that the firm takes product prices $P = (P_1, \dots, P_M) > 0$ and input prices $W = (W_1, \dots, W_N) > 0$ as given, and attempts to adjust outputs and inputs so as to solve $\max_{YX} \{PY - WX\}$. If $\{Y^*, X^*\}$ solves this problem, then the firm's profit function is $H(P, W) = PY^* - WX^*$. For competitive firms, the technology regularity conditions imply that the profit function is finite, nonnegative, real-valued, continuous, smooth, convex in prices, twice differentiable, and bounded. H is also linear homogeneous in prices. The firm's profit-maximizing product supply and factor demand equations can be obtained directly from the profit function by Hotelling's Lemma: $D_P H(P, W) = Y^*(P, W)$ and $D_W H(P, W) = -X^*(P, W)$, where D is the vector differential operator. Properties of the supply and demand equations are inherited directly from the properties of the profit function.

The multiproduct profit function in full static equilibrium is specified with a translog functional form as a second-order Taylor's series approximation around the unit price vector by [23]:⁴

$$\begin{aligned} \ln H = & A_0 + A_T T + A_{DA} \ln DA + \sum_{i \in F} A_i \ln P_i + \sum_{i \in F} \sum_{j \in F} A_{ij} \ln P_i \ln P_j \\ & + \sum_{i \in F} A_{iT} \ln P_i T + \sum_{i \in M} A_{iDA} \ln P_i \ln DA, \end{aligned} \quad (1)$$

where H is economic profit (total revenue less the costs of fuel and oil, capital services, and total opportunity cost of labor), P is an 8×1 vector of 5 strictly positive ex-vessel species prices for cod, haddock, yellowtail and other flounders, and a residual, all others, and 3 input prices for labor (including captain), energy, and capital services, T is an annual dummy variable for 1981, and DA is total otter trawl fleet days absent minus the days absent of each individual vessel (representing congestion and technical externalities). The resource stock provides a technological constraint since it is external to the firm, and is captured by the 1981 dummy variable (T). For simplicity, assume that ex ante expectations are realized ex post.

The revenue and cost share equations obtained by Hotelling's Lemma are

$$\frac{\partial \ln H}{\partial \ln P_i} = \frac{P_i Y_i}{H} = A_i + A_{iT} T + A_{iDA} \ln DA + \sum_{j \in F} A_{ij} \ln P_j, \quad \forall i \in M, N, \quad (2)$$

which are positive for outputs and negative for inputs. Without loss of generality, symmetry is imposed by $A_{ij} = A_{ji}$ for $i \neq j$ in (1) and (2). Equality between the parameters of the profit and share equations is maintained. Linear homogeneity in prices is imposed on the profit function by

$$\sum_i A_i = 1, \quad \sum_i A_{iT} = \sum_i A_{iDA} = \sum_i A_{ij} = \sum_j A_{ij} = \sum_i \sum_j A_{ij} = 0.$$

Econometric restrictions for separate production processes for each species or nonjointness in inputs and for the existence of a consistent aggregate input index for effort may be imposed on (1) and (2) and hypothesis tests performed. The likelihood

⁴In a few instances, a species was not landed by a vessel. Since with a translog form this introduces problems with the residuals, the value 0.01 is inserted.

ratio test is used for hypothesis testing.⁵ Nonjointness in inputs for all M species is tested first by the following econometric restriction at the point of approximation [12]: $A_{ij} = -A_i A_j$, $i \neq j$, $i, j \in M$.

Input-output separability implies composite indices for both catch and effort, and offers the most general test of effort's existence. If input-output separability is rejected, then a separate test for weak separability of all inputs is possible [29]. Denny and Fuss [11] state that the test for input-output separability with the translog form is an exact test for strong separability, and that failure to reject implies a Cobb-Douglas function of consistent translog aggregates for both catch and effort. The econometric restriction for input-output separability is no interaction between inputs and outputs: $A_{ij} = 0$, $i \neq j$, $i \in M$, $j \in N$.

The data set consists of 1980–1981 annual observations on 42 full-time otter trawlers with at least 85 days absent from port in each year. Home ports for the vessel and crew in each year are assigned by a plurality of days absent from port. All of the major New England ports are represented as well as a number of minor ports. The data set depicts the more productive vessels of the full-time near- and off-shore otter trawl fleet. This sector accounts for over 80% of the entire fleet's landings, and is therefore the most important for regulation and hypothesis testing. The mean sample vessel is 120 gross registered tons (GRT), has a crew size of 5, and is built in 1972. In contrast, the entire fleet's mean vessel is 70 GRT with 3 crew members. The mean sample vessel's days absent from port is 167, with a range of 85 to 249, and makes an average of 57 trips/yr of 3 days duration (with a range of 1 to 13 days). The sample vessels are typically larger and spend more time fishing than the mean fleet vessel.

All of the revenue, landings, and vessel and trip characteristics data are from the National Marine Fisheries Service (NMFS) Weighout File. Implicit ex-vessel species prices are formed by dividing total revenue by total pounds landed. Fuel and oil costs are from federal income tax returns. Most vessel acquisition prices (including hull, gear, equipment, and engine) are exact, compiled from receipts; the remainder are from federal tax returns. Both new and used vessels are included, although the majority are new vessels. Only those vessels purchased between late 1976 and 1979 are included in order to eliminate effects of vintage and structural changes in the industry. Because most of the sample consists of vessels participating in NMFS loan guarantee or capital construction fund programs, the vessels tend to be newer and more successful than most of the fleet. All data are proprietary and confidential.

The port-specific opportunity cost of labor provides an exogenous representation of returns to labor and food costs and is a Divisia index of separate opportunity costs for crew, engineer, and captain.⁶ Labor cost data are from the Bureau of

⁵The likelihood ratio is the ratio (L) of the restricted to unrestricted maximum value of the likelihood function. The test statistic formed by $-2 \ln L$ has an asymptotic distribution of chi-square with degrees of freedom equal to the number of independent restrictions.

⁶Since little reliable empirical evidence is available, it is assumed only that fishermen will work in the major port towns, which are predominately industrial and blue collar. The opportunity cost of labor per crew member is a Divisia index of the opportunity costs of ordinary crew members (mean annual income of total manufacturing), the mechanic (mean annual income of maintenance mechanic, machinery), and captain (annual income 20% higher than an ordinary seaman's). These indices vary by both crew size and port. Crew members are assigned to one of five New England coastal manufacturing cities (Portland, Gloucester, Boston, New Bedford, and Providence) by geographical proximity of their home ports (as determined by a plurality of days absent from port).

Labor Statistics, U.S. Department of Labor and from comparable state agencies. Energy costs include all sales taxes, while energy prices are port-specific. The capital services price is comprised of depreciation and the opportunity cost of capital. All taxes other than sales are income taxes, and are excluded from revenue and costs because of linear homogeneity in prices. All values are deflated by the GNP implicit price index.

The profit function (1) has an additive disturbance term due to approximation error, while the revenue and cost share equations (2) have additive disturbances from errors in optimization [8]. Since the share equations sum to unity, the energy consumption equation is dropped and its parameters identified through linear homogeneity and symmetry constraints. The system (1) and (2) is estimated jointly by maximum likelihood.

3. THE EXISTENCE OF EFFORT AND JOINT PRODUCTION

Table I presents the estimated parameters of the model. The systems R^2 is 0.94, while the OLS R^2 values for the share equations range from 0.27 to 0.40, with 0.89 for the profit function.⁷ The predicted share equations are positive for outputs and negative for inputs over all sample values, indicating monotonicity is satisfied. Own-price parameters with t -ratios larger than two in absolute value all display the correct algebraic signs. The restricted profit function is not convex at the point of approximation, however, and parameter estimates and tests may consequently be inconsistent with expectations of the competitive model.⁸ Nevertheless, Wales [33] notes that violation of regularity conditions such as convexity need not imply the absence of an underlying optimization process, but may simply reflect the limitations of flexible functional forms to approximate the true function over the range of the data.

The hypotheses test results for nonjointness in inputs and input-output separability are now considered. A 5% level of overall significance is assumed. Nonjointness in inputs is rejected, since the chi-square statistic is 34.79, while the 5% critical value is 18.31 with 10 independent restrictions. The production technology exhibits jointness in inputs, so that separate harvesting process are not implied for the five species and all inputs are required to produce all outputs. Since the technology is in long-run equilibrium, the jointness arises from an interdependent production process. Input-output separability is not rejected, since the chi-square test statistic is 20.31, while the 5% critical value is 24.99 with 15 independent restrictions. These results indicate a Cobb-Douglas functional form of consistent translog aggregates for total catch and effort, joint-in-inputs production, and thereby provide firm-level support for the traditional bioeconomic model. A consistent fishing effort index following neoclassical production theory can now be formed.

⁷The system R^2 is calculated as $1 - \exp[2(L_1 - L_2)/N]$, where L_1 (L_2) is the maximum value of the log-likelihood when all the slope coefficients are zero (unconstrained), and N is the total number of observations [4].

⁸Since convexity is implied by the assumption of profit maximization, any violation of this condition is a serious weakness in the performance of the model.

TABLE I
Parameter Estimates of Long-Run Translog Profit Function

Exogenous variables	Product shares				Factor shares			
	Cod	Haddock	Yellowtail flounder	Other flounders	All others	Capital services	Labor	Fuel ^a
Share	-18.8674 ^b	-25.7970 ^b	-0.3011	36.8349 ^b	15.4113 ^b	-2.7941 ^b	-15.6646	12.1780
Intercept	(5.7215)	(4.9191)	(3.2219)	(6.9472)	(7.7352)	(0.2030)	(12.7929)	
1981 Share	5.3492 ^b	8.0111 ^b	0.2321	-7.7949 ^b	-1.0693	0.1245	0.0001	-4.8528
Dummy	(1.5619)	(1.4224)	(0.9104)	(1.9788)	(2.2174)	(0.0969)	(0.0001)	
Cod	-0.0065	0.0257	0.0661	-0.1313	0.0523	0.0593	0.0619	-0.1275
	(0.1011)	(0.0504)	(0.0412)	(0.1744)	(0.0768)	(0.0569)	(0.1582)	
Haddock		-0.0076	-0.0756 ^b	0.0260	0.1145	0.0184	-0.0872	-0.0142
		(0.0323)	(0.0312)	(0.0841)	(0.0639)	(0.0376)	(0.0654)	
Yellowtail			0.1005 ^b	-0.0144	-0.0175	-0.0123	0.0006	0.0474
Flounder			(0.0156)	(0.0768)	(0.0413)	(0.0327)	(0.0612)	
Other				1.2767 ^b	0.5501 ^b	-0.1757 ^b	-0.7863 ^b	-0.7451
Flounders				(0.2313)	(0.1541)	(0.0669)	(0.1569)	
All	(Symmetric)				0.4097 ^b	-0.3023 ^b	-0.6223 ^b	-0.1845
Others					(0.0469)	(0.0744)	(0.1191)	
Capital						-0.1550 ^b	0.3500 ^b	0.2177
Services						(0.0189)	(0.0392)	
Labor							-0.3530 ^b	1.4363
							(0.0360)	
Fuel								-0.6301
Fleet days	-436.5281 ^b	-645.6365 ^b	-17.8143	592.0388 ^b	95.6826			
Absent	(123.7660)	(112.7426)	(72.3341)	(156.7265)	(177.7570)			

Profit function intercept -5.3619 (9.5457)

Profit function 1981 dummy 8.5922^b (3.0288)

Profit function fleet days absent -840.3241^b (218.9021)

Note Long-run translog profit function with equality, symmetry, and linear homogeneity as maintained hypotheses. Asymptotic standard errors in parentheses.

^aThe parameters in the fuel share equation are calculated using the constraints implied by linear homogeneity and symmetry.

^bStatistically significant at 5%.

4. FISHING EFFORT INDEX

Previous empirical studies estimating or employing fishing effort have specified ad hoc representations of technology, neglected energy, and specified restrictive functional forms such as the Cobb-Douglas.⁹ Effort is typically represented as some variant of fishing time or days absent from port multiplicatively adjusted by a productivity measure, fishing power. In more recent studies, fishing power is a production function with stock proxy specifications of labor and capital (generally leading to biases). In some instances, fishing power is determined by regressing total catch (without regard to consistent aggregation) upon factors of production. Energy

⁹Cunningham and Whitmarsh, Anderson, and Clark provide bibliographies of many empirical studies, which are not presented here for the sake of brevity. These limitations apply to all stages of optimization in most bioeconomic models. A functional form is termed flexible if it can provide a second-order approximation to an arbitrary function. The Cobb-Douglas form imposes homogeneity, strong separability, and elasticities of substitution of one.

consumption is neglected. Relative productivities across vessel types and/or classes are then compared. However, simultaneity bias exists if effort determined in this manner is then specified as an aggregate input in a yield-effort equation.

Specification of a flexible functional form relaxes several hypotheses maintained with the linear and Cobb-Douglas forms previously employed. Moreover, Fuss [15] indicates that predictions of a dependent variable (such as fishing effort) from a flexible functional form provide superlative indices.¹⁰ Predictions from the translog provide a superlative index equivalent to the Tornquist discrete approximation to the Divisia. These predictions can serve as instrumental variables in the multistage optimization implicit to most bioeconomic models. Simultaneous equation bias is then eliminated in subsequent stages of decision making, since fishing effort is now exogenous in these later stages. Alternatively, a superlative index is used in a revenue function or supply response framework where the level of effort is endogenously determined [24], or if effort is used to examine relative resource abundance or industry productivity.

Estimating a translog production function for effort allows construction of a consistent effort index. The translog form follows from the profit function results, which suggest a translog aggregate for effort; although not developed here, a translog consistent aggregate for total catch or revenue could also be formed. The translog production function for effort (E) specified as a second-order Taylor's series approximation to an arbitrary underlying production function about the geometric mean of the data (since all variables are scaled by their geometric means) becomes:¹¹

$$\ln E = \ln B_0 + \sum_{r \in N} B_r \ln X_r + \sum_{r \in N} \sum_{s \in N} B_{rs} \ln X_r X_s + \sum_{r \in N} B_{rT} \ln X_r T, \quad (3)$$

where symmetry is imposed by $B_{rs} = B_{sr}$, $s \neq r$. T again represents a 1981 dummy variable, and X_r represents input r . The approximation error is assumed to be negligible. Assuming competitive factor markets and efficient production, differentiation of (3) with respect to the logarithms of inputs provides cost share equations [5]: $M_r = \partial \ln E / \partial \ln X_r = B_r + B_{rT} + \sum_{s \in N} B_{rs} \ln X_s$, $\forall r \in N$, where M_r is the relative share of input r in total cost. Constant returns to scale is required to create a consistent effort index [30]. Constant returns to scale is directly imposed by [5]: $\sum_{r \in N} B_r = 1$, $\sum_{r \in N} B_{rs} = 0$, $\forall s \in N$.

The specified variables include crew-days-fished (L), ton-days-absent (K), energy consumption (F), and a 1981 dummy variable (T).¹² The resource stock again

¹⁰ Numerous index number formulae can be explicitly derived from particular aggregator functions. The resulting index is termed exact for that particular aggregator function. Index numbers that are exact for flexible aggregator functions are called superlative [14].

¹¹ Boisvert [7] demonstrates that the important characteristics of the translog production function evaluated at the geometric mean are identical to those of the exact translog production function because the Taylor expansion around zero is equivalent to scaling the data around the geometric mean. Estimation of a translog unit cost function to obtain the price of effort was not successful. However, using Fisher's weak factor reversal test and the estimated quantity index from eq. (3), an implicit Tornqvist price of effort index can be constructed.

¹² The labor and capital flow specifications are suggested by Jim Kirkley. Crew size includes captain. Ton-days-absent provides an adequate measure of the are of influence over which the gear extends, since larger vessels have the potential to fish a greater area than smaller vessels and are less constrained by inclement weather and sea conditions.

provides a technological constraint. Since the cost share equations sum to unity, the capital share equation is dropped, and the labor and energy share equations estimated,

$$\begin{aligned} M_L &= B_L + B_{LT} + B_{LL} \ln L + B_{LK} \ln K + B_{LF} \ln F, \\ M_F &= B_F + B_{FT} + B_{LF} \ln L + B_{KF} \ln K + B_{FF} \ln F. \end{aligned} \quad (4)$$

Following Berndt and Christensen, a stochastic specification is adopted which reflects errors in optimizing behavior. The equations are estimated as a system by maximum likelihood. The data are again from the National Marine Fisheries Service, federal income tax returns, and vessel acquisition receipts. Energy consumption is obtained by dividing energy costs by port-specific energy prices. Materials are an insignificant proportion of total input costs and usage.

Berndt and Christensen show that the Allen partial elasticity of substitution (AES) can be specified as: $AES_{rs} = |G_{rs}|/|G|$, where $|G|$ is the determinant of the bordered matrix whose rs th element has the form $G_{rs} = A_{rs} + M_r M_s$ and whose r th diagonal element has the form $G_{rr} = A_{rr} + M_r(M_r - 1)$. The matrix is bordered by the factor shares. Berndt and Christensen provide further details. These Hicksian elasticities represent pure substitution effects, since they are calculated for a given level (not necessarily optimal) of effort.

5. THE INTERNAL STRUCTURE OF EFFORT AND FISHERIES MANAGEMENT

Public regulation of fishing industries is extended to correct for market failure arising from an open-access resource. Like all other open-access resources, fish stocks tend to be overexploited. The resulting inefficient resource allocation and loss of economic rents are usually redressed by regulation of production, particularly management of fishing effort [2, 9, 25, 28]. Regulating the level of the effort in turn requires empirical knowledge of the internal structure of effort, that is, the relationships among the individual factors of production comprising effort. Management agencies can apply this knowledge to assess the technological constraints to firms as the latter respond to regulation and changes in market conditions. Regulatory bodies can then tailor their policies to better achieve their goals. Effective restrictions on some but not all inputs may also induce expansion of unregulated inputs, which can cause inefficient factor proportions [13, 32].

The estimated Allen elasticities of substitution can provide this information on the internal structure of effort. Moreover, the limited empirical applicability and reliability of bioeconomic models of multispecies fisheries, restrictive specification of the production technology, oversimplified and deterministic population dynamics, and limited regulatory power of regulatory agencies suggest that elasticities of factor substitution of firms may be of more reliable and immediate use to practical multispecies fisheries management than the results from aggregate or industry bioeconomic models.

Parameter estimates for the translog cost share equations appear in Table II. The estimated parameters of the capital share equation are derived from the symmetry and linear homogeneity restrictions. The bordered principal minors of the bordered Hessian matrix indicate a negative definite quadratic form and strictly convex

TABLE II
Parameter Estimates of Translog Effort Function

Exogenous variables	Labor	Energy	Capital ^a
Share intercept	0.383 ^b (0.015)	0.296 ^b (0.009)	0.321
1981 share dummy	-0.020 (0.021)	-0.025 (0.013)	0.045
Labor	-0.057 ^b (0.010)	-0.011 (0.008)	0.068
Energy		0.077 ^b (0.012)	-0.020
Capital	(Symmetric)		-0.048

Note. Asymptotic standard errors in parentheses.

^aParameters calculated from the symmetry and linear homogeneity constraints.

^b*t*-ratios greater than 1.96.

isoquants at the geometric mean of the sample. There are no a priori restrictions on the algebraic signs of the second-order terms. The 'large' *t*-ratios for energy parameters suggest that fishing effort functions have been misspecified and parameter estimates biased by the omission of energy [32].

The null hypothesis that the underlying production function for effort has the simple Cobb-Douglas form is examined by a likelihood ratio test. The value of the test statistic is 31.75, while the chi-square value with 3 degrees of freedom at the 5% significance level is 7.81. The null hypothesis is decisively rejected, suggesting that previous effort functions employing a Cobb-Douglas functional form may have unnecessarily maintained restrictive hypotheses upon the structure of production (although this is an empirical question determined on a case-by-case basis).

The 1980 Allen partial elasticities of factor substitution are reported in Table III. Since the elasticities are not independent of input levels, they are calculated at the geometric mean of the data set. Standard errors are not presented, since each elasticity is a nonlinear function of all the first and second partial derivatives of the production function. The Allen partial elasticities of substitution indicate that all three inputs, capital, labor, and energy, are substitutes and are generally elastic. The inelastic AES between capital and labor indicates limited substitution possibilities, but otherwise the substitution possibilities are elastic between labor and energy and capital and energy. The own-price factor demand elasticities for all three inputs are negative as expected, and are all elastic, especially capital and labor.

TABLE III
1980 Own-Price Elasticities of Factor Demand and Allen
Partial Elasticities of Substitution

Item	Labor	Capital	Energy
Labor	-1.643	0.726	1.946
Capital		-2.821	2.125
Energy			-4.033

The generally elastic substitution possibilities between capital, energy, and labor suggest a rather series potential for expansion of unregulated inputs. Inefficient factor proportions are then possible, and management might need to regulate more than one input. For example, capital can be regulated to reduce the level of effort in the industry, such as the current policy of limiting mesh size or restricting ultra free entry or market contestability through limiting vessel numbers. Reducing effort may reduce open-access social inefficiency, but might also induce inefficient factor proportions of firms by unanticipated expansions in crew size or energy consumption if fishermen substitute the unregulated inputs for the regulated input, capital. Strand *et al.* [32] present the only other study which empirically estimates measures of multifactor substitution with a functional form that places no prior restrictions on elasticities of substitution, the transcendental. They measure similar multi-factor substitution possibilities in the Atlantic surf clam industry. Through observation, other researchers indicate similar findings by reporting unanticipated factor substitution in many fisheries [20, 27]. Potential gains in social efficiency may then be dissipated through increases in costs [25].

The problem of unanticipated factor substitution and economic inefficiency is unimportant if factor complementarity or inelastic factor substitution possibilities exist. Otherwise, public regulation ostensibly might regulate all the individual inputs comprising effort. However, social and cultural factors and regulatory costs (and in New England, New Bedford union resistance) are likely to make this management approach difficult to implement. Moreover, Anderson's [3] recent theoretical analysis demonstrates that in some cases there are potential rent gains to regulating some but not all factors even if there is factor substitution. Practical fishery management in New England and other fisheries might therefore want to regulate the most easily monitored and enforced input; the current New England plan of managing mesh size is certainly consistent with this regulatory approach.

Regulatory programs limiting the number of vessels often experience not only unanticipated factor substitution of unregulated inputs, but increases in the quantity of capital [2, 20, 25, 27, 28, 32]. In this manner, fishermen attempt to capture any increases in rents arising from regulation. The reported elastic own-price demand for capital indicates that if a limited access program were to be implemented in New England, that similar to other fisheries, an increase in productive capacity is likely to be experienced. The elastic own-price demand for capital also suggests that the problem of capital expansion could be potentially serious. Any limited entry program implemented in New England may want to consider limitations on capital other than simply the number of vessels.

The internal structure of fishing effort also provides technological constraints important for industrial policies. The general elastic capital-labor-energy substitutability suggests that maintenance of U.S. energy prices below world levels encourages inefficient input usage and possibly socially suboptimal pressures on the resource through inducing increases in the level of fishing effort. Policies designed to reduce energy consumption by promoting substitution with other inputs can be counterproductive. Moreover, industry relief through financial assistance programs which lower the real interest rate to fishermen may increase the level of fishing effort beyond the social optimum. Similarly, policies designed to increase industry productivity through capital expansion may increase usage of all inputs and expand pressure on the resource stock. For example, Karpoff [19] reports that government financial assistance to purchase fishing assets such as a limited entry license or

capital can induce expansion. Alternatively, policies designed to lessen pressures on energy markets, such as investment tax credits, may encourage a fleet expansion which places socially suboptimal pressures on the resource stock that would remain after problems in energy markets have abated. The industry is also likely to retain surplus labor with stagnant real wages and high unemployment in the old and industrially torpid New England port cities due to the elastic labor demand with respect to the opportunity cost of labor. Finally, the fuel price shocks and subsequent high interest rates of recent years may have also induced substantial factor substitution.

CONCLUSIONS

Although production technology plays a pivotal role in fisheries economics and management, several important hypotheses are traditionally maintained upon its structure. Fishing effort is implicitly specified to be a consistent composite index of the individual factors of production formed as an intermediate input in a multistage decision making process. The production technology in multispecies fishing industries is also traditionally assumed to be joint in inputs in bioeconomic models, while fishery managers often assume that individual production processes exist. This paper rigorously addresses these issues and provides a means by which to empirically test the structure of production for the existence of fishing effort and joint-in-inputs production. This paper also demonstrates the theoretically proper manner by which to construct a consistent effort index which can then be used in bioeconomic models, industry performance studies of relative resource abundance and productivity, and public regulation of production. These concepts are developed in an empirical study of the New England otter trawl industry.

REFERENCES

1. L. Anderson, The relationship between firm and industry in common property fisheries, *Land Econom.* **52**, 179–191 (1976).
2. L. Anderson, "The Economics of Fisheries Management," The Johns Hopkins Press, Baltimore (1977).
3. L. Anderson, Potential economic benefits from gear restrictions and license limitation in fisheries regulation, *Land Econom.* **61**, 409–418 (1985).
4. N. Baxter and J. Cragg, Corporate choice among long-term financing instruments, *Rev. Econom. Statist.* **52**, 225–235 (1970).
5. E. Berndt and L. Christensen, The translog function and the substitution of equipment structures and labor in U.S. manufacturing 1929–68, *J. Econom.* **1**, 81–114 (1973).
6. C. Blackorby, D. Primont, and R. Russell, "Duality, Separability, and Functional Structure: Theory and Economic Applications," North-Holland, New York (1978).
7. R. Boisvert, The translog production function: Its properties, its several interpretations and estimation problems, in *Agri. Econom. Research*, Dept. of Agricultural Economics, Cornell University (1982).
8. D. Burgess, Duality theory and pitfalls in the specification of technologies, *J. Econom.* **3**, 105–121 (1975).
9. C. Clark, "Mathematical Bioeconomics: The Optimal Management of Renewable Resources," Wiley, New York (1976).
10. S. Cunningham and D. Whitmarsh, Fishing effort and fisheries policy, *Mar. Policy* **4**, 309–316 (1980).

11. M. Denny and M. Fuss, The use of approximation analysis to test for separability and the existence of consistent aggregates, *Amer. Econom. Rev.* **67**, 404–418 (1977).
12. M. Denny and C. Pinto, An aggregate model with multi-product technologies, in "Production Economics: A Dual Approach to Theory and Applications" (M. Fuss and D. McFadden, Eds.), Vol. II, North-Holland, Amsterdam (1978).
13. A. DeVany, W. Gramm, T. Saving, and C. Smithson, The impact of input regulation: The case of the U.S. dental industry, *J. Law Econom.* **20**, 367–381 (1982).
14. E. Diewert, Exact and superlative index numbers, *J. Econom.* **4**, 115–145 (1982).
15. M. Fuss, The demand for energy in Canadian manufacturing: An example of the estimation of production structures with many inputs, *J. Econom.* **5**, 89–116 (1977).
16. J. Hof, R. Lee, A. Dyer, and B. Kent, An analysis of joint costs in a managed forest ecosystem, *J. Environ. Econom. Management* **12**, 338–352 (1985).
17. D. Huang and C. Lee, Toward a general model of fishery production, *S. Econom. J.* **43**, 846–854 (1976).
18. R. Just, D. Zilberman, and E. Hochman, Estimation of multicrop production functions, *Amer. J. Agri. Econom.* **65**, 770–780 (1983).
19. J. Karpoff, Low-interest loans and the markets for limited-entry permits in the Alaska salmon fisheries, *Land Econom.* **60**, 69–80 (1984).
20. E. Keen, Limited entry in the case of the Japanese tuna fishery, in "Ocean Fishery Management: Discussions and Research" (A. Sokoloski, Ed.), Dept. of Commerce NOAA Tech. Rep. CIRC-371, Seattle (1973).
21. N. Kulatilaka, Are observed technologies at long-run equilibrium? Tests on the validity of static equilibrium models, *J. Econom.* **25**, 253–268 (1985).
22. L. Lau, Applications of profit functions, in "Production Economics: A Dual Approach to Theory and Applications" (M. Fuss and D. McFadden, Eds.), Vol. 1, North-Holland, Amsterdam (1978).
23. R. Lopez, Structural implications of a class of flexible functional forms for profit functions, *Internat. Econom. Rev.* **26**, 593–601 (1985).
24. R. McGaw, The supply of effort in a fishery, *Appl. Econom.* **13**, 245–253 (1981).
25. K. McConnell and V. Norton, Fisheries management schemes, in "Limited Entry as a Fisheries Management Tool" (R. Rettig and J. Ginter, Eds.) Univ. of Washington Press, Seattle (1978).
26. P. Moss and D. Terkla, Income and employment change in the New England fishing industry, *Ocean Develop. Internat. Law* **15**, 37–59 (1985).
27. P. Pearse and J. Wilen, Impact of Canada's Pacific salmon fleet control program, *J. Fisheries, Research Board Canad.* **36**, 764–769 (1979).
28. A. Scott, Development of economic theory on fisheries regulation, *J. Fisheries, Research Board Canad.* **36**, 725–741 (1979).
29. R. Shumway, Supply, demand, and technology in a multiproduct industry: Texas field crops, *Amer. J. Agri. Econom.* **65**, 748–760 (1983).
30. R. Solow, The production function and the theory of capital, *Rev. Econom. Stud.* **23**, 101–108 (1955).
31. D. Squires, Long-run profit functions for multiproduct firms, *Amer. J. Agri. Econom.* (in press).
32. I. Strand, Jr., J. Kirkley, and K. McConnell, Economic analysis and the management of Atlantic surf clams, in "Economic Analysis for Fisheries Management Plans" (L. Anderson Ed.), Ann Arbor Science, Ann Arbor (1981).
33. T. Wales, On the flexibility of flexible functional forms: An empirical approach, *J. Econom.* **5**, 183–193 (1977).
34. J. Wilson, Adaptation to uncertainty and small numbers exchange: The New England fresh fish market, *Bell J. Econom.* **11**, 491–504 (1980).

Long-Run Profit Functions for Multiproduct Firms

Dale Squires

A long-run specification of the multiproduct profit function is developed from the restricted profit function. The multiproduct restricted profit function and the envelope condition are used to estimate the optimal, long-run levels of the quasi-fixed factor. Formulas for long-run Marshallian elasticities of substitution and transformation, economies of scope, product-specific and overall economies of scale, and economic measures of capacity utilization are developed for the translog functional form. The methodology is illustrated by a case study of the New England otter trawl industry.

Key words: economic capacity utilization, fisheries, long-run, profit functions, multiproduct costs and technology

This article extends the full static equilibrium and restricted (or variable) multiproduct profit functions (Shumway, McKay, Lawrence, and Vlastuin; Lopez 1984, 1985a, b; Weaver) to a long-run specification of technology in which all quasi-fixed inputs are at their optimal, long-run equilibrium levels. Many studies of long-run technology specify a cost function with a single, exogenously determined and constant output (Kulatilaka, Brown and Christensen). In contrast, the long-run multiproduct profit function allows all products (as well as quasi-fixed inputs) to be endogenous without the simultaneous equation econometric problems or assumptions of homothetic separability otherwise required for long-run cost functions. This cost function procedure also ignores the adjustment of output levels to changes in product and factor prices and technology over the long run.

Primary emphasis in this article is upon a comprehensive and unified presentation of the long-run structure of technology and costs when products are multiple and decision vari-

ables to firms. The presentation develops Marshallian elasticities of substitution and transformation. The multiproduct profit function is also extended to consider the structure of long-run multiproduct costs, including long-run economies of scope and product-specific and multiproduct returns to scale. The profit function has previously been used only to examine the structure of production, while cost function studies of multiproduct costs have assumed full static equilibrium and constant outputs. The long-run multiproduct profit function is further developed to provide a measure of economic capacity utilization; previous studies employ single-product cost functions (Schankerman and Nadiri, Morrison 1985, in press). The method is demonstrated with data on the New England otter trawl fleet.

The Long-Run Multiproduct Profit Function

The next two sections consider the limitations to dynamic models, the advantages of long-run models, and develops the long-run profit function.

Long-Run and Dynamic Models

Dynamic specifications of production technology are increasingly advanced in response to the recognized limitations of static models.¹

¹ Berndt, Morrison, and Watkins; Brown and Christensen, Schankerman and Nadiri; and Kulatilaka provide additional sum-

Dale Squires is an economist with the National Marine Fisheries Service, La Jolla, and at the time of manuscript preparation, a lecturer, Department of Economics, San Diego State University, where model estimation was completed.

Conversations with Bob Halvorsen, Nalin Kulatilaka, Randall Brown, Catherine Morrison, Dan Huppert, Alec MacCall, Kathy Segerson, and Rick Methot are gratefully acknowledged. The comments and suggestions by Jim Kirkley and two referees have improved the paper and are also gratefully acknowledged. Lorraine Prescott very patiently typed the paper. Any errors remain the responsibility of the author. The results do not necessarily reflect position of the National Marine Fisheries Service.

The most recent approach posits dynamic equilibrium models in which the costs of adjustment are explicitly specified and the firm assumed to be continuously in dynamic rather than static equilibrium. The firm is assumed to face smooth, convex costs of adjusting the stocks of quasi-fixed inputs. An intertemporal cost minimization or profit maximization problem is solved to provide explicit time paths of the quasi-fixed factors. This offers insights into the intertemporal factor substitution possibilities (Lopez 1985b; LeBlanc and Hrubovcak; Berndt, Morrison, and Watkins).

These dynamic equilibrium models have several limitations. They are empirically difficult to apply and have demanding data requirements. Long time series of data are required, and degrees of freedom and powers of tests can be limited. The assumption of smooth, convex costs of adjustment circumscribes asymmetries between investment and disinvestment costs. The internal adjustment costs are the only assumed cause of disequilibrium. Differences between actual and static equilibrium levels of quasi-fixed factors may arise for reasons other than smooth convex internal costs of adjustment, such as institutional rigidities, credit rationing, or physical immobility of input changes (such as lags or irreversibility), or regulatory restrictions. For example, regulatory restrictions hindering capital mobility or credit rationing are commonly found in agriculture and marine fishing industries, so that application of dynamic models requires particular care. Dynamic equilibrium might then be a misspecification.

The restricted (or partial) equilibrium framework developed by Lau, Mork, and later by Brown and Christensen, offers an attractive alternative. Others (Schankerman and Nadiri, Kulatilaka, Morrison 1985, Halvorsen and Smith, Hazilla and Kopp) have subsequently applied the approach in the framework of single-product cost functions. The firm is assumed to be in static equilibrium with respect to a subset of variable inputs conditional upon the observed levels of the quasi-fixed factors. The long-run optimal levels of the quasi-fixed factors are endogenously derived. The restricted and long-run profit functions describe the technology and costs of the

temporary and long-run equilibriums, respectively.

The restricted equilibrium approach includes both dynamic equilibrium and other departures from full static equilibrium, yet the empirical and conceptual complications are obviated.² Unlike the current generation of dynamic equilibrium models, the adjustment process can accommodate any factors causing disequilibrium. Explicit specification of the adjustment process is not required, but the firm's intertemporal behavior (such as the time path of quasi-fixed factors and dynamic substitution and transformation possibilities) is not explained. Nonetheless, an important difference between the short-run and long-run elasticities indicates slow adjustments of the quasi-fixed factors. The model is fundamentally static because future levels of the quasi-fixed factors are not affected by past departure from long-run equilibrium.

This long-run approach is particularly valuable for firm-level studies. Panel data sets typically do not include sufficiently long time series for dynamic models, and both balanced and unbalanced panel data sets and fixed effects are readily accommodated. The long-run procedure does not necessarily require a time series of data and therefore allows analysis from cross-sectional data of the long-run structures of costs and technology (which the dynamic procedure does not offer). The long-run approach is also useful in studies of production technology in natural resource industries because a model dynamic in the production technology should also be dynamic in the resource stock. The restricted equilibrium procedure is thus a practical method for estimating the long-run (multiproduct) technology given firm-level, cross-sectional, or panel data. The restricted equilibrium approach is also conceptually and empirically more general and flexible than the dynamic equilibrium approach.

Long-Run Profit Function

The long-run multiproduct profit function is developed from the restricted profit function. The multiproduct restricted profit function is specified as $HR(P; Z)$, where HR equals re-

maries and discussions in the context of single-product cost function. Appelbaum and Harris provide an alternative intertemporal approach based upon a neo-Austrian framework.

² Multistage optimization of inputs or outputs may also occur under homothetic separability. Full static equilibrium is assumed for these subsets.

stricted profit (total revenue less total variable costs), P is a $V \times 1$ vector of strictly positive prices, and Z represents an $F \times 1$ vector of positive levels of quasi-fixed factors. By Hotellings lemma: $\nabla_p HR = Y(P; Z)$, where ∇ is the vector differential operator, Y is a $V \times 1$ vector of M positive outputs and N negative variable inputs, and provides conditional output supply and conditional variable input demand equations.

Hotelling's lemma further states (Lau): $\nabla_Z HR = -P'_Z$, where P'_Z is the vector of shadow prices of the quasi-fixed factors, Z . This term indicates the increase in restricted profits for a unit increase in the level of the quasi-fixed factors. If the firm optimizes with respect to the quasi-fixed factors, the variable inputs and outputs, and is in long-run equilibrium, then by the envelope condition the shadow prices equal the market rental prices of the quasi-fixed factors, P_Z (Samuelson):³ $\nabla_Z HR = -P_Z$.

The long-run multiproduct profit function H is derived from the restricted profit function HR . For given levels of quasi-fixed factors, the total multiproduct profit function is specified: $HT(P, P_Z, Z) = HR(P, P_Z; Z) -$

stricted profit-maximizing levels. The first-order condition for maximizing HT with respect to Z is given by the envelope condition. Solving this condition for the optimal, long-run level of Z , $Z^* = Z^*(P, P_Z)$ and substituting into total profit, HT , gives the long-run multiproduct function H :

$$(1) \quad H(P, P_Z) = HR[P, Z^*(P, P_Z)] - P'_Z Z^*(P, P_Z).$$

Long-Run Marshallian Elasticities

The long-run elasticities of substitution and transformation are (Kulatilaka):

$$(2) \quad E_{ij} = \partial \ln Y_i(Z^*) / \partial \ln P_j \quad i, j \in V, F$$

where $Y_i(Z^*)$ is the long-run supply (demand) of product (input) i , $Y_i(Z^*) > 0$ for outputs, and $Y_i(Z^*) < 0$ for inputs. These are Marshallian elasticities since they include both expansion and pure substitution effects. Their derivation follows that presented in Kulatilaka, Halvorsen and Smith, and Brown and Christensen, so that only their final form is presented. All elasticities are evaluated at Z^* .

$$(3) \quad E_{ii} = \frac{(A_{ii} + S_i^2 - S_i)}{S_i} - \frac{(A_{iZ} + S_i S_Z)^2}{S_i(A_{ZZ} + S_Z^2 - S_Z)} \quad i \in V$$

$$(4) \quad E_{ij} = \frac{(A_{ij} + S_i S_j)}{S_i} - \frac{(A_{iZ} + S_i S_Z)(A_{jZ} + S_j S_Z)}{S_i(A_{ZZ} + S_Z^2 - S_Z)} \quad i, j \in V$$

$$(5) \quad E_{ii} = \frac{S_Z}{(A_{ZZ} + S_Z^2 - S_Z)} \quad i \in F$$

$$(6) \quad E_{ij} = \frac{S_Z(A_{jZ} + S_j S_Z)}{S_i(A_{ZZ} + S_Z^2 - S_Z)} \quad i \in V, j \in F$$

$$(7) \quad E_{ij} = \frac{(A_{jZ} + S_j S_Z)}{(A_{ZZ} + S_Z^2 - S_Z)} \quad i \in F, j \in V.$$

$P'_Z Z$, where P'_Z is the transpose of P_Z and HT is total maximum profit. The long-run profit function H is obtained by first maximizing HR conditional upon the level of Z and then maximizing HT with respect to Z , holding the first V outputs and variable inputs at their re-

Marshallian elasticities derived from the multiproduct restricted profit function estimated with or without the envelope condition are conditional upon the quantity of Z (which is not necessarily optimal). These conditional elasticities do not allow for the effects from induced changes in Z . The formulas for these elasticities for variable inputs and outputs are given by the first terms of equations (3) and (4). The second term in (3) is negative for products and positive for inputs by concavity of the restricted profit function in Z (Lau). The

³ The long run is defined as the state where total profits (restricted profits less the costs of the quasi-fixed inputs) are maximized. The long run so defined is merely a construct to distinguish the observed short-run equilibrium from the desired long-run equilibrium and need never be actually achieved by the observed technology (Kulatilaka).

restricted own-price elasticities are therefore smaller in absolute value than the long-run elasticities, which is consistent with LeChatelier's principle. The long-run cross-price elasticities can differ in absolute magnitude in either direction because the second term in (4) can be either positive or negative for both inputs and outputs.

The Structure of Long-Run Multiproduct Costs

The long-run profit function can also be extended to examine the structure of multiproduct costs. This approach relaxes the maintained hypotheses of the static cost function: exogenously determined products and full static equilibrium of all inputs. Instead, the long-run structure of multiproduct costs is evaluated at the optimal levels of all outputs (and inputs) rather than exogenously determined (not necessarily optimal) levels.

Economies of Scope

An important multiproduct cost measure is economies of scope. Economies of scope measures the effects of joint production upon costs. Production which is joint in inputs has a lower cost than independent production of several products (Baumol, Panzar, and Willig).

Two sources of jointness in inputs, and therefore economies of scope, exist: an interdependent production process and allocatable (quasi-) fixed factors. An interdependent production process leads to economies of scope through local cost complementarity; higher levels of one output reduce the marginal costs of other products. Local cost complementarity can arise from several sources, such as risk minimization, the quasi-public nature and lumpiness of capital, economies of networking, the reuse of an input by more than one product, and the high costs of obtaining information and the organizational and strategic impediments to its market transfer (Sharkey, Bailey and Friedlaender). Allocatable (quasi-) fixed factors yield jointness (Shumway, Pope, and Nash), hence economies of scope, when the marginal allocation of variable inputs depends upon the allocation of the fixed input, and generate product-specific fixed costs.

Gorman extends the work of Baumol, Pan-

zar, and Willig to establish the relationship between cost complementarity and product-specific fixed costs in determining economies of scope. Gorman shows that, even in the absence of cost complementarity, the existence of subadditive fixed costs is a sufficient condition for economies of scope:

$$(8) \quad c_{ij} - [F(S) + F(T) - F(S \cup T)]/Y_i Y_j \leq 0,$$

where c_{ij} denotes the second derivatives of the variable cost function with respect to outputs i and j , $F(S)$ and $F(T)$ are the product-specific fixed costs of the disjoint product sets S and T , and $F(S \cup T)$ is the fixed cost of producing both sets together as a single product set. When there are no product-specific fixed costs, $C_{ij} < 0$ is a sufficient condition for economies of scope, where C represents static equilibrium or long-run multiproduct costs.

Condition (8) implicitly assumes allocatable (quasi-) fixed factors in order to obtain the terms involving product-specific fixed costs. However, in a long-run competitive equilibrium at the firm level, this source of jointness disappears. Shumway, Pope, and Nash (p. 77) state if a competitive equilibrium exists for the (quasi-) fixed factors and the market rental rate equals the shadow price of these factors, then the effects of jointness from allocatable (quasi-) fixed factors vanish. Shumway, Pope, and Nash also note that the dual specification of technology (required to test for economies of scope) cannot yield product-specific demand equations for either the variable inputs or the fixed allocatable inputs, it can only identify total demand equations for each input.⁴ As a consequence, the long-run equilibrium levels of the (quasi-) fixed allocatable inputs, and therefore product-specific fixed costs, cannot be determined by a long-run cost or profit function. Thus, condition (8) should be considered as a short- or intermediate-term test for economies of scope. Also, the condition (8) for economies of scope in the long run becomes a test for local cost complementarity ($C_{ij} < 0$), and the long-run source of jointness

⁴ Since Shumway, Pope, and Nash note that the dual approach is limited when allocatable (quasi-) fixed factors exist, the condition (8) provides a difficult test for a cost function even in the short run. Moreover, use of the static cost function to directly measure overall economies of scope captures only cost complementarities if product-specific fixed costs do not exist, that is, fixed factors are not allocable.

in inputs for the firm is an interdependent production process.

The condition for long-run cost complementarity based on the long-run multiproduct profit function is developed using the results of Lau and Lopez (1984). Lopez indicates the following relationship between the Hessian matrix of the cost function C and the Hessian of the profit function: $H = C_{ij} = H_{ij}^{-1}$, $i \neq j$, i, j are outputs, where C_{ij} is the second partial derivative of C with respect to products i and j , and H_{ij}^{-1} represents the inverse of the second partial derivative of H with respect to the product prices of i and j . Lau relates the derivatives of the long-run (H) and restricted (HR) profit functions, allowing all forms entering H_{ij}^{-1} to be derived from the restricted profit function: $H_{ij} = HR_{ij} - (HR_{ZZ})^{-1}HR_{iZ}HR_{Zj}$, where all terms are defined as before. The derivatives required to evaluate the inverse of this expression with the translog form are derived in the same manner as the Marshallian elasticities. The condition for local cost complementarity with the long-run translog multiproduct profit function is

$$(9) \quad H_{ij}^{-1} = \left[\frac{HR}{P_i P_j} (A_{ij} - S_i S_j) - (A_{ik} + S_i S_k)(A_{jk} + S_j S_k) / (A_{kk} + S_k^2 - S_k) \right]^{-1}.$$

Only the internal brackets require evaluation since $HR, P_i, P_j > 0$. Predicted shares (S_i) are evaluated at Z^* . The test is applied equation-by-equation rather than simultaneously for the system, and it is not a statistical test.

Product-Specific Economies of Scale

Product-specific economies of scale measure the change in costs through variations in the output of one product while holding the quantities of other products constant. Although product-specific economies of scale cannot be directly measured by the translog profit function, a sufficient condition is obtained by examining incremental marginal costs (Baumol, Panzar, and Willig). C_{ii} less (greater) than zero implies decreasing (increasing) long-run product-specific economies of scale for product i . Since $C_{ii} = H_{ii}^{-1}$, the following sufficient condition with the translog form provides the basis for this nonstatistical test:

$$(10) \quad H_{ii}^{-1} = \left[\frac{HR}{P_i^2} (A_{ii} + S_i^2 - S_i) - (A_{ik} - S_i S_k)^2 / (A_{kk} + S_k^2 - S_k) \right]^{-1}.$$

Only the terms in the internal brackets require evaluation since $HR, P_i > 0$. $C_{ii} < 0$ implies decreasing marginal and average incremental cost curves for product i . Under marginal cost pricing, the revenues collected from the sale of product i fall short of the incremental costs of their production (Baumol, Panzer, and Willig), but MacDonald and Slivinski note that overall efficiency may imply what appears to be inefficiencies within the diversified firm. This test can also be applied to single-product profit functions.

Cost Convexity

The diagonal elements of the Hessian submatrix, $C_{ii} = \partial^2 C / \partial Y_i$, all $i \in M$, represent product-specific marginal cost curves, while the off-diagonal elements C_{ij} indicate cost complementarities among product pairs. Convexity of the long-run cost function (inherent in the long-run profit function) in outputs can be tested by examining this Hessian submatrix for outputs.

Long-Run Multiproduct Returns to Scale

Long-run multiproduct or ray returns to scale for the profit function measure the behavior of costs for proportional changes in total firm output and all variable and quasi-fixed inputs.⁵ This is a straightforward extension of the concept of single-product scale economies, where the output composition remains fixed while its scale can vary. The degree of long-run ray scale economies equals the ratio between long-run production costs and the revenues that occur with marginal cost pricing. The rev-

⁵ The single-product profit function is not well defined for constant or increasing returns to scale. However, the multiproduct profit function does not suffer from this limitation because the structures of multiproduct costs and industry are dependent upon both the scale and composition of outputs. Even if ray returns to scale are increasing for the existing division of products, the multiproduct cost structure may be such that some other division of outputs among smaller firms may provide an even more efficient form of multiproduct industry organization. In fact, cost subadditivity is required for a single multiproduct firm (natural monopoly), and increasing ray returns to scale provides only a sufficient condition for ray subadditivity. Shaeffer shows that multiproduct functions should in both theory and practice cause downward bias in estimated ray scale economies.

enues exceed, are less than, or equal long-run costs as there are decreasing, increasing, or locally constant long-run ray returns to scale.

Long-run multiproduct economies of scale are a weighted sum of long-run economies of scope and long-run product-specific economies of scale (Baumol, Panzer, and Willig; Bailey and Friedlaender):

$$(11) \quad S_M = \frac{w_T S_T + (1 - w_T) S_{M-T}}{1 - SC_T},$$

where the product set M is partitioned into two disjoint subsets T and $M - T$, SC_T is the measure of long-run economies of scope, S_T and S_{M-T} are measures of long-run product-specific economies of scale, and $W_T = (\sum_T Y_i C_i / \sum_M Y_i C_i)$. The degree of long-run overall scale economies for both product sets is thus a weighted average of long-run product-specific scale economies magnified by long-run economies of scope through the denominator. Long-run ray returns to scale can still be captured even if decreasing long-run product-specific returns to scale exist throughout the product set. Long-run overall returns to scale with the long-run translog multiproduct profit function are measured by $(\sum_N S_i + \sum_F S_F) / (\sum_M S_j)$, where all shares are predictions evaluated at Z^* . Because measurement is taken along the expansion path, this is also a measure of long-run overall size economies.

Capacity Utilization Measurement

The long-run profit function can also be applied to studies of economic capacity utilization (CU) when product levels and mixes are decision variables to firms. Recent applications of the long-run single-product cost function to CU measurement can be extended to the long-run multiproduct profit function (Morrison 1985, Schankerman and Nadiri). The effects of changes in product and factor prices on CU measurement and temporary equilibria when outputs are endogenous are directly captured by the multiproduct profit function. In contrast, biased measures of economic CU are likely from single-product cost functions for multiproduct firms after the exogenous shocks inducing the new, temporary equilibrium, unless outputs are separable because CU measures will be on a new product ray.

Noncompetitive product markets are readily accommodated by the approach of Die-

wert. Although not developed here, CU measures based on the long-run multiproduct profit function can be used to adjust productivity measurements for departures from full equilibrium (Morrison 1985, Schankerman and Nadiri).

Capacity utilization measures represent the proportion of available productive capacity currently utilized. Economic measures of CU based on the primal depict the divergence between short-run temporary equilibrium (Y) and long-run full equilibrium (Y^*) levels of outputs, so that $CU = Y/Y^*$ in product space. In the general case of long-run nonconstant returns to scale, the capacity level of outputs Y^* for some product combination corresponds to the tangency of the short-run ray (SRAC) and long-run ray (LRAC) average cost curves. These capacity output levels are in steady state in that the firm has no incentive to change product levels and combinations from Y^* . Since the stocks of quasi-fixed factors position and influence the shape of SRAC, Y^* and CU explicitly reflect short-run constraints (Morrison 1985).

Morrison, and Schankerman and Nadiri provide a dual interpretation of economic CU measures using the cost function. Dual CU measures contain information on the difference between the long-run competitive equilibrium and temporary equilibrium in terms of implicit costs of being away from long-run equilibrium. These disequilibrium costs with the profit function are opportunity costs in terms of restricted or variable profit foregone with the divergence from long-run equilibrium. This measure not only accounts for cyclical changes in the economy, but in natural resource industries, changes in the level and mix of resource availability.

The implicit costs of disequilibria are represented by the difference between the shadow price of the quasi-fixed factor (say capital), P_z^* , and the market rental price, P_z . When the capital stock is inadequate relative to demand, $P_z^* > P_z$; that is, the valuation of an incremental unit of capital stock is high, or conversely, the opportunity cost in terms of restricted profit foregone of having too low a capital stock is high. Alternatively, when $Z^* > Z$ and $P_z^* < P_z$, the marginal unit of capital has a low valuation relative to its market value. This is an opportunity cost of too high a level of capital. The economic CU measure will exceed one when $Y > Y^*$ (and thus $P_z^* > P_z$) and will fall short when the reverse holds (Morrison 1985).

Morrison's (1985) specification of the dual shadow-value measure of *CU* adapted for the long-run profit function becomes⁶

$$(12) \quad 1 + \frac{Z[P_z^* - P_z]}{HR}.$$

With a homothetic technology (so that the scale impact of all inputs is the same) and nonconstant returns to scale, the measure $(1/S_M)(1 + Z[P_z^* - P_z]/HR)$ can also be calculated, where S_M is the measure of ray scale economies calculated at Z . This measure provides the savings at Y from increasing Z to a steady-state level.

The multiproduct profit function measure of economic capacity utilization allows product levels to be endogenous. The output levels determined by the restricted profit function are endogenous and conditional upon the existing stock of capital, Z , and are thus not the output levels to which Z will adjust in reaching a steady state. Morrison notes, however, that this is not a problem for *CU* calculation, since *CU* is a short-run notion, so that the existing output levels remain the valid short-run levels for comparative purposes.

Empirical Analysis

This section specifies a translog profit function for estimation, discusses the data, and reports the long-run structures of multiproduct costs and technology.

Empirical Specification

Otter trawlers are fishing vessels which drag a net at the stern or side of the vessel. Otter trawlers often harvest multiple species with the levels and mix of catch as decision variables of the firms. Outputs are endogenous because vessels choose species and locations to target. These multiple products are produced by organizing fuel, labor, and capital (vessel, engine, gear, and equipment). Fishing firms are therefore multiproduct firms producing a vector of endogenous products from a vector of endogenous inputs. This endogeneity suggests that a multiproduct profit function rather than a cost or revenue function is the appro-

priate dual representation of the firm's production technology. Moreover, the large number of vessels in the industry, presence of important auction markets, homogenous products, and minimal vertical and horizontal integration among firms assure exogenously determined product prices. Input prices are exogenous because inputs are traded on regional or even national markets.

The translog multiproduct restricted profit function is specified as a second-order Taylor's series approximation by:⁷

$$(13) \quad \ln HR = A_0 + A_T T + \sum_i A_i \ln P_i + \sum_k A_k \ln Z_k + \sum_i \sum_j A_{ij} \ln P_i \ln P_j + \sum_k \sum_l A_{kl} \ln Z_k \ln Z_l + \sum_i \sum_k A_{ik} \ln P_i \ln Z_k + \sum_i A_{iT} \ln P_i T,$$

where T is an index of time, and without loss of generality, symmetry is imposed by $A_{ij} = A_{ji}$ for $i \neq j$ and $A_{kl} = A_{lk}$ for $k \neq l$, and $A_{ik} = A_{ki}$ for $i \neq k$.

The conditional revenue and cost-share equations obtained by Hotelling's lemma are

$$(14) \quad \frac{\partial \ln HR}{\partial \ln P_i} = \frac{P_i Y_i}{HR} = A_i + A_{iT} T + \sum_j A_{ij} \ln P_j + \sum_k A_{ik} \ln Z_k, \quad \forall i \in M, N,$$

which are positive for outputs and negative for inputs. Linear homogeneity in prices is imposed on the multiproduct restricted profit function by the restrictions: $\sum_i A_i = 1$, $\sum_i A_{ij} = \sum_j A_{ij} = \sum_i A_{ik} = \sum_k A_{ik} = 0$. All *ex ante* expectations are assumed realized *ex post*.

This study specifies three species groups

⁶ Alternatively, the *CU* measure (12) can be interpreted as a ratio of short- and long-run ray returns to scale (Morrison, in press).

⁷ All functional forms for multiproduct functions are limited. The global approximation capacity of the Fourier form is attractive (especially for tests of cost subadditivity), but typically requires a prohibitively large number of estimated parameters. The large regular region and ability to impose many nonnegative sign restrictions before loss of flexibility make the minflex and full Laurent forms attractive but similarly require an extensive number of observations. The generalized McFadden allows easy imposition of convexity, but is not easy to estimate. Lopez (1985a) demonstrates that flexible forms linear in profits a priori impose quasi-homotheticity, input-output separability in multiproduct technologies and additive separability in inputs. The forms using a Box-Cox transformation allow for linear profits and assume a particular form of non-normal disturbances prior to transformation.

($M = 3$), roundfish (cod and haddock), flatfish (yellowtail and other flounders), and a residual, all others; roundfish and flatfish are formed by division indices. Two variable inputs are specified ($N = 2$), energy (fuel and oil) consumption and labor (including captain). One quasi-fixed factor ($F = 1$) is specified, capital, represented by the vessel's gross registered tonnage (*GRT*). Short-run economic profit is therefore total revenue less the opportunity cost of labor and energy costs; T represents a dummy variable for 1981, where the base period is 1980. Resource abundance is specified as a technological constraint because it is beyond the control of any individual firm but nevertheless affects the production environment within which the firm operates. That is, capital, labor, and energy are organized by firms and applied to the natural resources. Changes in resource abundance may then be viewed as shifts in the production technology that relates the generation of outputs from inputs, i.e., changes in an efficiency parameter (McFadden). These changes are represented by the 1981 dummy variable.

The restricted profit function (13) is jointly estimated with the restricted revenue and cost share equations (14), and all equations have additive disturbances due to errors in optimization. The restrictions for symmetry and linear homogeneity in prices are directly imposed. Because the restricted share equations sum to unity, the energy consumption equation is dropped and its parameters identified through the linear homogeneity and symmetry restrictions. The system of equations is estimated by the iterative seemingly unrelated regression technique. The estimates are consistent, asymptotically normal, equal to maximum likelihood estimates, and are invariant to choice of deleted equation.⁸

The balanced panel data set consists of annual observations for two years, 1980 and 1981, on forty-two full-time otter trawl vessels with at least 85 days absent from port in each year. Home ports are in all of the major and most minor New England ports. Home ports are assigned by a plurality of days absent. The range of sample space almost completely en-

compasses the population of full-time vessels in this sector. The mean sample vessel is 120 gross registered tons (*GRT*), has a crew size of five, and was built in 1972. The mean of the sample vessel's days absent from port is 167, with a range of 85 to 249. The average vessel makes an average of fifty-seven trips per year of three days' duration (with a range of 1 to 13 days).

The revenue, landing, vessel, and trip characteristics data are from the National Marine Fisheries Service (NMFS) Weighout File. Fuel and oil costs are from federal income tax returns. Most vessel acquisition prices (hull, engine, gear, and equipment) are without measurement error because they are compiled from bills-of-sale; the remainder are from federal income tax returns. Both new and used vessels are included, but only those purchased between late 1976 and 1979 are used in order to eliminate effects of vintage and structural changes in the fishery from the Fishery Conservation and Management Act of 1976. All data are confidential. Because the fuel cost and vessel acquisition price data are from NMFS capital construction fund or guaranteed loan program participants, the sample is likely to reflect some of the more successful and newer vessels.

Returns to captain and crew are determined after each fishing trip by the vessel lay system, which normally yields payments as a percentage of gross or net trip revenue. By this system, net trip returns are apportioned by formulas which can vary by port and sometimes vessel. In this study, returns to labor are assigned an exogenous economic valuation through use of the opportunity cost of labor. This provides an exogenous representation of returns to labor and food costs per person.⁹ The opportunity cost of ordinary crew members is the mean annual wage of total manufacturing, the opportunity cost of a vessel engineer is the mean annual wage of a maintenance mechanic, machinery, and the opportunity cost of the captain is a mean annual wage rate 20% higher than an ordinary seaman's to reflect the captain's entrepreneurial and managerial skills. Crew members are assigned to one of five New England coastal manufacturing cities (Portland, Gloucester, Boston, New Bedford, and Provi-

⁸ The approach illustrated by McKay, Lawrence, and Vlastuin estimates the variable and fixed cost share equations by the Zellner technique, which requires all the regressors to be exogenous. Since the dependent variables of the fixed input share equations include the fixed inputs, (iterative) three-stages least squares may be more appropriate.

⁹ The opportunity cost approach to valuing labor has been used by Clark and Munro for marine fishing industries and Lopez (1984) for family farm labor.

Table 1. Parameter Estimates of Translog Restricted Profit Function

Exogenous Variables	Product Shares			Factor Shares		Profit Function
	Roundfish	Flatfish	All Others	Labor	Fuel ^a	
Share intercept	-4.486 ^b (1.637) ^c	2.512 (1.491)	-0.208 (0.639)	0.434 (0.623)	2.749 ^b (1.337)	10.7375 ^b (3.346)
1981 share dummy	-0.071 (0.084)	-0.002 (0.069)	0.184 ^b (0.080)	-0.064 (0.061)	-0.047 (0.039)	0.617 (0.608)
Roundfish	-0.252 (0.207)	-0.155 (0.105)	-0.115 ^b (0.058)	0.275 (0.145)	0.247 ^b (0.124)	
Flatfish		0.233 (0.207)	-0.051 (0.045)	-0.052 (0.128)	0.025 (0.102)	
All others			0.097 ^b (0.035)	0.036 (0.042)	0.033 (0.026)	
Labor	(symmetric)			-0.048 (0.049)	-0.211 (0.310)	
Fuel					-0.093 (0.332)	
Gross registered tons	0.426 ^b (0.075)	-0.319 ^b (0.057)	0.010 (0.086)	0.016 (0.053)	-0.134 ^b (0.033)	0.296 (0.781)
Gross registered tons squared						0.035 (0.063)

^a Parameter estimates derived from the constraints implied by linear homogeneity and symmetry. Standard errors are computed as first-order Taylor's series approximations.

^b Statistically significant at 5%.

^c Standard errors are in parentheses.

dence) by geographical proximity to their home ports. The opportunity cost of labor is a divisia index of the separate opportunity costs for crew, engineer, and captain which varies by port and crew size. Labor cost data are from the U.S. Department of Labor, Bureau of Labor Statistics, and from comparable state agencies. All profits are therefore economic profits. Energy costs include all sales taxes, while energy prices are port-specific. The capital services price is comprised of the opportunity cost of capital and depreciation. Because all restrictions are directly imposed upon the profit function, prices are deflated by the gross national product (GNP) implicit price index.

Empirical Results

The estimated parameters of the translog multiproduct restricted profit function are presented in table 1. The systems R^2 (Baxter and Cragg) is 0.99, while the OLS R^2 s for the share equations are 0.66 for roundfish, 0.51 for flatfish, 0.30 for all others, and 0.08 for labor. The predicted share equations are consistent with monotonicity over all sample values. The restricted profit function is not convex, although this is not a statistical test. A test of convexity cannot be interpreted as strictly a test of profit maximization because convexity can be violated for a number of other reasons.

For example, Wales shows that the estimates of a flexible functional form may violate convexity even if the data come from a perfectly well-behaved technology. Linear aggregation of the other species assemblage can also cause the apparent failure of convexity.

The optimal capital stock, Z^* , represented by the vessel's gross registered tons (GRT), can be solved from the equation $\nabla_z HR = P_Z$ using the 1980 arithmetic sample mean real service price per ton (GRT) and evaluated at the point of approximation. Because a closed form analytical solution is not possible with the translog function, a numerical solution is required. The solved value for mean Z^* in the open-access fishery is 99.96, while the observed sample mean value is 120.38.

The divergence between observed Z and estimated Z^* might simply reflect sampling error in the estimated Z^* . A number of hypothesis testing procedures for static equilibrium are possible. Bootstrap and jackknife procedures can be used. Schankerman and Nadiri apply Hausman's test for specification error in a system of simultaneous equations. Kulatilaka applies the delta method to obtain a first-order Taylor's series approximation for the variance of Z^* to form a t -test. Kulatilaka's test in quantity space is

$$(15) \quad t = (Z^* - Z)/[V(Z^*)]^{1/2},$$

Table 2. 1980 Long-Run Marshallian Elasticities

Price	Roundfish	Flatfish	All Others	Labor	Fuel	Capital
Roundfish	3.36	0.06	2.36	1.77	3.87	3.88
Flatfish	0.03	0.01	0.13	0.54	0.09	-0.32
All others	0.61	0.05	-0.06	0.35	0.22	0.54
Labor	-0.75	-0.37	-0.58	-1.56	-0.64	-0.73
Fuel	-1.06	-0.04	-0.68	-0.14	-1.18	-1.14
Capital	-2.19	0.29	-1.17	-0.97	-2.36	-2.23

which is t -distributed, $V(Z^*) = Z_A^* V(A) Z_A^{*'} A$, A is the vector of estimated parameters and therefore a random variable, Z_A^* is a vector of partial derivatives of Z^* with respect to A , and $Z_A^{*'} = -[HR_{ZZ}]^{-1} HR_{ZA}$ evaluated at Z^* .

The estimated t is -0.80 , implying no statistically significant difference between Z and Z^* . This test result may reflect a robust level of Z^* in an industry in which fishermen make long-run investment decisions with expectations of important cyclical and stochastic temporal and spatial fluctuations in resource abundance (Gold). Vessels of a certain size and design are also required to harvest different fishing grounds in different seasons and in the stormy northwest Atlantic waters. The lumpiness and long life of capital in marine fishing industries may further contribute toward the robust Z^* . Moreover, important used and new vessel markets, vessel leaseings, and deliberate vessel sinkings for insurance exist, and otter trawlers are mobile and can easily switch to a gear, location, or targeted species other than those of the owner's original intentions.¹⁰

Table 2 reports that long-run Marshallian elasticities evaluated at the 1980 arithmetic sample mean and $Z^* = Z = 120.38$ GRT.¹¹ The own-price supply elasticities all have the expected algebraic signs except for all others.¹² The own-price supply elasticities for

flatfish and all others are both inelastic, while that for roundfish is quite elastic. All cross-price supply elasticities are positive, indicating complementarity, and are inelastic except in one instance. The inelasticities and complementarities reflect the mixed species nature of the groundfishery, the somewhat limited capability of the otter trawl gear and electronics to target different species, and the distinct spatial distribution of many bottom-dwelling finfish species. Search costs in the form of energy consumption, risk, quality deterioration for some species, and opportunity costs of catch foregone and labor also limit harvesting responsiveness to changes in species prices. The marginal search costs quickly outweigh the incremental revenues obtained.

The long-run factor demands are all elastic and negative as expected. The inputs are all Marshallian complements, most with inelastic cross-price elasticities, perhaps caused by expansion effects outweighing pure substitution effects. Sakai indicates that all inputs can be Marshallian complements because of expansion effects. The elastic long-run factor demands suggest that fishermen are very responsive to fuel price and interest rate shocks such as those of the preceding decade.

The long-run elasticities between inputs and outputs display the expected signs, with increases in product prices leading to increased factor demand and increases in factor prices inducing decreased product supply. These elasticities for flatfish and all others are usually inelastic. They are elastic for roundfish, reflecting the pivotal importance of the ubiquitous cod and haddock as the traditional mainstays of the fishery. Moreover, the generally elastic output responses for capital suggest that the species composition may be particularly impacted by changes in interest rates.

¹⁰ Although the 20% difference in Z^* and observed Z is not statistically significant, it may nonetheless indicate a 20% overcapitalization of the average firm. The interpretation is consistent with the overcapitalization expected to be found in an open-access fishing industry.

¹¹ The long-run Marshallian elasticities change only minimally when evaluated at $K^* = 99.96$ GRT. Because the observed levels of the quasi-fixed input coincide with the desired levels, the restricted and full static equilibrium models are equivalent and there is thus no need to estimate a full static equilibrium model.

¹² The negative sign for all others may be due to aggregation bias, since more than 50 different minor species are linearly aggregated over all trips in each year for each vessel. Linear aggregation technologies imply perfect transformation among outputs. This may be the factor which leads to the absence of convexity. Alternatively, since all measures of incremental marginal costs and product-specific economies of scale are evaluated at the long-

run, optimal levels of outputs and inputs, the increasing product-specific returns to scale for all others and declining average incremental costs imply a declining supply curve for the other species assemblage. This may be caused by a mining down of the resource stock, which includes species that are at high abundance.

The long-run measures of local cost-complementarity evaluated at the 1980 arithmetic sample mean for the observed capital stock are 33.78 for roundfish-flatfish, 1.54 for roundfish-all others, and 21.23 for flatfish-all others. Economies of scope do not exist between any of the product pairs. This absence may be due to the spatial distribution of different fish stocks, the importance of fishing skill in harvesting, and the quasi-public but lumpy nature of fishing boats. Long-run incremental marginal costs are 0.35 for roundfish, 204.08 for flatfish, and -100.00 for all others. These results suggest the presence of decreasing product-specific returns to scale for roundfish and flatfish and increasing product-specific returns to scale for all others. Cost advantages exist to harvesting additional species in this latter category, and firms specializing in harvesting these species are likely (vessels with the Point Judith, Rhode Island cooperative provide an example). Evaluation of the hessian matrix for outputs of the long-run cost function does not indicate convexity.

The 1980 estimate of long-run overall returns to size is 0.65, indicating decreasing ray returns to scale. Cost or profit advantages do not exist to expanding production if product proportions are held constant when all prices and resource abundance are fixed. As the scale of production expands for a given level and mix of the resource stock, vessels harvest in increasingly marginal fishing grounds, further deplete the fish stocks in existing grounds, harvest in more adverse weather, and so on. The absence of economies of scope throughout the product set contributes toward the decreasing ray returns. Moreover, Gold states that "materials dominated" processes are those in which the controlling constraint on output capabilities is the richness of the natural resources utilized or processed, such as the population density of fishing grounds. It may well then be that the measure of long-run overall (and product-specific) returns to scale is altered by changes in the composition and level of resource abundance and density; Kirkley provides empirical support for this thesis with a multiproduct revenue function.

Since the existing capital stock Z is found to be at the optimal long-run level Z^* , the economic CU measure is one. Partitioning observed productivity changes into potential or long-run productivity growth and the effects of temporary equilibrium would not be necessary for any productivity measures. The im-

portance of testing divergences from full static equilibrium are also apparent.

Concluding Comments

The restricted multiproduct profit function in conjunction with the envelope condition allows a long-run analysis of the structures of production and costs without prior assumptions of full static equilibrium and exogenous products. A recent test for economies of scope is also shown to hold only in the short term and may be difficult to implement even with restricted cost functions. Long-run models are also shown to have certain advantages over dynamic models in many potential applications. Measures of economic captivity utilization in multiproduct industries are also shown to be generally more suitable from profit functions and likely to be biased if determined from single-product cost functions. It is also important to test for economic CU measures diverging from one.

The framework is developed for vessel-level data from the New England otter trawl fleet. Product supply elasticities are typically inelastic, and most species are complements in harvesting. Factor demand elasticities are both elastic and inelastic, and all inputs are Marshallian complements. Economies of scope and product-specific economies of scale are generally absent and overall returns to scale are decreasing. Not surprisingly, the industry is primarily composed of single-vessel firms with minimal horizontal and vertical integration. The long-run cost function is also not convex with respect to products.

[Received March 1986; final revision received February 1987.]

References

- Appelbaum, E., and R. Harris. "Estimating Technology in an Intertemporal Framework: A Neo-Austrian Approach." *Rev. Econ. and Statist.* 59(1972):161-70.
- Bailey, E., and A. Friedlaender. "Market Structure of Multiproduct Industries." *J. Econ. Lit.* 20 (1982):1024-48.
- Baumol, W., J. Panzar, and R. Willig. *Contestable Markets and the Theory of Industry Structure*. San Diego CA: Harcourt Brace & Co., 1982.

- Baxter, N., and J. Cragg. "Corporate Choice among Long-Term Financing Instruments." *Rev. Econ. and Statist.* 52(1970):225-35.
- Berndt, E., C. Morrison, and G. Watkins. "Dynamic Models of Energy Demand: An Assessment and Comparison." *Modeling and Measuring Natural Resource Substitution*, ed. E. Berndt and B. Field. Cambridge MA: MIT Press, 1981.
- Brown, R., and L. Christensen. "Estimating Elasticities of Substitution in a Model of Partial Static Equilibrium: An Application to U.S. Agriculture, 1947 to 1974." *Modeling and Measuring Natural Resource Substitution*, ed. E. Berndt and B. Field. Cambridge MA: MIT Press, 1981.
- Clark, C., and G. Munro. "Fisheries and the Processing Sector: Some Implications for Management Policy." *Bell J. Econ.* 11(1980):603-16.
- Diewert, W. E. "Duality Approaches to Microeconomic Theory." *Handbook of Mathematical Economics*, vol. 2, ed. K. Arrow and M. Intriligator. Amsterdam: North-Holland Publishing Co., 1982.
- Gold, B. "Changing Perspectives on Size, Scale, and Returns: An Interpretive Survey." *J. Econ. Lit.* 19 (1981):5-33.
- Gorman, I. "Conditions for Economies of Scope in the Presence of Fixed Costs." *Rand. J. Econ.* 16 (1985):431-36.
- Halvorsen, R., and T. Smith. "Substitution Possibilities for Unpriced Natural Resources: Restricted Cost Functions for the Canadian Metal Mining Industry." *Rev. Econ. and Statist.* 68(1986):398-405.
- Hazilla, M., and R. Kopp. "Testing for Separable Functional Structure Using Partial Equilibrium Models." *J. Econometrics*, in press.
- Kirkley, J. "The Relationship between Management and the Technology in a Multi-Species Fishery: The New England, Georges Bank, Multi-Species Fishery." Ph.D. thesis, University of Maryland, 1986.
- Kulatilaka, N. "Are Observed Technologies at Long-Run Equilibrium? Tests on the Validity of Static Equilibrium Models." *J. Econometrics* 25(1985):253-68.
- Lau, L. "A Characterization of the Normalized Restricted Profit Function." *J. Econ. Theory* 12 (1976):131-63.
- LeBlanc, M., and J. Hrubovcak. "Dynamic Input Demand: An Application to Agriculture." *Appl. Econ.* 18(1986):807-18.
- Lopez, R. "Estimating Substitution and Expansion Effects Using a Profit Function Framework." *Amer. J. Agr. Econ.* 66(1984):358-67.
- . "Structural Implications of a Class of Flexible Functional Forms for Profit Functions." *Int. Econ. Rev.* 26(1985a):593-601.
- . "Supply and Investment in the Canadian Food Processing Industry." *Amer. J. Agr. Econ.* 67 (1985b):40-48.
- MacDonald, G., and A. Slivinski. "A Positive Analysis of Multiproduct Firms in Market Equilibrium." Rochester Ctr. for Econ. Res. Work. Pap. No. 16, University of Rochester, 1985.
- McFadden, D. "Cost, Revenue, and Profit Functions." *Production Economics: A Dual Approach to Theory and Applications*, vol. 1, ed. M. Fuss and D. McFadden. Amsterdam: North-Holland Publishing Co., 1978.
- McKay, L., D. Lawrence, and C. Vlastuin. "Profit, Output Supply, and Input Demand Functions for Multiproduct Firms: The Case of Australian Agriculture." *Int. Econ. Rev.* 24(1983):323-39.
- Mork, K. "The Aggregate Demand for Primary Energy in the Short and Long Run for the U.S. 1949-75." Rep. No. MIT-EL 78-007 WP, Massachusetts Institute of Technology, 1978.
- Morrison, C. "Primal and Dual Capacity Utilization: An Application to Productivity Measurement in the U.S. Automobile Industry." *J. Bus. and Econ. Statist.* 3(1985):312-24.
- . "Productivity Measurement with Nonstatic Expectations and Varying Capacity Utilization: An Integrated Approach." *J. Econometrics*, in press.
- Sakai, Y. "Substitution and Expansion Effects in Production Theory: The Case of Joint Production." *J. Econ. Theory* 9(1974):255-74.
- Samuelson, P. "Prices of Factors and Goods in General Equilibrium." *Rev. Econ. Stud.* 21(1953):1-20.
- Schankerman, M., and I. Nadiri. "Restricted Cost Functions and the Rate of Return to Quasi-Fixed Factors, with an Application to R&D and Capital in the Bell System." *J. Econometrics*, in press.
- Shaffer, Sherrill. "Scale Economies in Multiproduct Firms." *Bull. Econ. Res.* 36(1984):51-58.
- Sharkey, W. *The Theory of Natural Monopoly*. Cambridge: Cambridge University Press, 1982.
- Shumway, C. "Supply, Demand, and Technology in a Multiproduct Industry: Texas Field Crops." *Amer. J. Agr. Econ.* 65(1983):748-60.
- Shumway, C., R. Pope, and E. Nash. "Allocatable Fixed Inputs and Jointness in Agricultural Production: Implications for Economic Modeling." *Amer. J. Agr. Econ.* 66(1984):72-78.
- Wales, T. "On the Flexibility of Flexible Functional Forms, An Empirical Approach." *J. Econometrics* 5(1977):183-93.
- Weaver, R. "Multiple Input, Multiple Output Production Choices and Technology in the U.S. Wheat Region." *Amer. J. Agr. Econ.* 65(1983):45-56.

Public regulation and the structure of production in multiproduct industries: an application to the New England otter trawl industry

Dale Squires*

This article considers the problem of managing multispecies fishing industries as one of regulating the production of individual multiproduct firms. The multispecies New England otter trawl industry is examined within this framework. Empirical results derived from estimating a multiproduct profit function indicate that management consistent with the structures of multiproduct production and costs would directly regulate inputs. Little support is provided for applying the traditional bioeconomic model to the fishery studied.

1. Introduction

■ Public regulation of multispecies fishing industries is imposed to correct for market failure arising from an open-access resource. Like other open-access resources, fish stocks tend to be overexploited. The resulting inefficient resource allocation and loss of economic rents are usually redressed by regulating production. These attempts at public regulation, however, are likely to be disappointing because of a failure to recognize the management problem as one of regulating the production of individual multiproduct firms. Public regulation instead focuses at the industry level and either attempts to manage an aggregate input, fishing effort, and total industry catch, or targets individual species and inputs while neglecting their technological and cost interrelationships. The formulation of public regulation of production in multispecies fishing industries thus faces a conceptual problem, and such policies should be based on sound empirical knowledge of the firm-level structure of production and costs. Regulatory agencies can apply this knowledge to assess the technological and cost conditions facing individual firms, and the agencies can thereby tailor their policies better to achieve their goals.

The New England otter trawl industry¹ provides an example of a multispecies fishing industry in which failure to recognize the management task as one of regulating the pro-

* National Marine Fisheries Service and San Diego State University.

The comments of Sam Pooley, Pedro Alba, Dan Huppert, Jon Conrad, Robert Mendelsohn, and James Kirkley are gratefully acknowledged. The very helpful assistance of Alvin Klevorick and two anonymous reviewers has substantially improved the article. Any errors remain the responsibility of the author. Lorraine Prescott has demonstrated patience throughout preparation of the article. The article does not necessarily reflect the position of the National Marine Fisheries Service.

¹ Otter trawling involves dragging a net at the stern or side of a vessel. Large otter boards and floats on the top mouth and weights on the bottom mouth keep the net open. After a period of time, the net is hauled in and its catch released onto the deck.

duction of multiproduct firms contributed to ineffective regulation. The Magnuson Fisheries Conservation and Management Act (hereafter the Magnuson Act) of 1976 charged eight regional fishery management councils with public regulation of their regional fishing industries. The New England Fishery Management Council introduced a management plan in 1977 for the three most important species in its otter trawl fishery: cod, haddock, and yellowtail flounder. Although the plan evolved over time, it principally consisted of catch quotas for individual species and closures of particular fishing grounds. The plan placed possibly undue emphasis upon output regulation and relied upon controls that were often too intricate to implement and to enforce consistently. Most importantly, individual species were regulated as if each was harvested in a separate production process with no technological and cost interrelationships. Quotas were continually shortened in time (from annual to quarterly to trip) to prevent the entire quota from being harvested at the start of each time period. These limitations reduced profits, increased discards of fish caught beyond the quota level, and led to unexpected substitution of species in harvesting.

Thus, public regulation of this multispecies fishery failed, in part, because of an imperfect understanding of multiproduct production at the level of the firm and limited empirical information on the firm's transformation and substitution possibilities. The result was increasing political resentment and widespread evasion of the regulations. By 1980 an important reduction of the regulatory burden was experienced, and by 1981 enforcement was certainly at a minimum as preparation for the Interim Plan began.²

This study addresses this relationship between public regulation of inputs and outputs and the structure of multiproduct production in the multispecies New England otter trawl industry. Particular attention is given to the complexities of multiproduct technology to be addressed by regulation. Moreover, although the multiproduct cost structure is usually more important to regulation of market structure, knowledge of firms' costs does allow regulation of production to promote efficient production and multiproduct industry structure, and is developed in this study. Implications for the specification of bioeconomic models of fisheries are also provided. Since regulating the production of multiproduct firms is important to public regulation of industries other than fishing, the general procedure developed in this study has broad application.

The next section provides a background to the industry. Section 3 introduces the empirical model and describes the data. Section 4 examines the formal relationship between regulation of inputs and outputs and the structures of multiproduct production and costs. Section 5 reports the empirical results and considers the implications for public regulation, and the last section contains concluding remarks.

2. The industry

■ The New England otter trawl industry exploits some of the world's most valuable fishing grounds. Few firms are horizontally integrated to include more than one vessel, and individual owners operate most vessels. Vertical integration between shore-side processors and vessels also remains limited. The most important species harvested (in order of value) are cod, yellowtail and other flounders, haddock, redfish, and pollock. Cod is widely distributed over all the fishing grounds, and cod and haddock have traditionally formed the mainstay of the industry.

A number of ports dot the coast, each of which has developed a singular reputation. Rockland and Portland in Maine and Gloucester in Massachusetts are generally recognized

² Personal communication, Dr. Guy Marchesseault, Deputy Executive Director, New England Fishery Management Council. Some industry observers, such as Dr. James Wilson, Chair of the Statistical and Scientific Committee of the Council, believe that even by 1980, regulation was in fact virtually absent. The Interim Plan includes limited area closures for spawning and mesh size limitations, but not quotas.

as cod, haddock, pollock, and redfish ports; Boston as a cod and haddock port; Provincetown and New Bedford in Massachusetts as flounder ports; and Port Judith in Rhode Island as a port of underutilized species such as scup and butterfish. Distances and access to fishing grounds also vary by port and contribute toward port specializations. Rockland and Portland vessels tend to fish in the Gulf of Maine, New Bedford and Provincetown vessels off Georges Bank, Gloucester trawlers off both, and Point Judith trawlers in southern New England and Georges Bank waters.

Fishermen of all ports are free to land their harvests at any port offering the highest price. This option, however, must be balanced against the additional travel time, market transaction costs, and personal and financial relationships existing between many fishermen and fish buyers. New Bedford and Boston contain important auction markets for landings (Wilson, 1980).

The vessel is one of the most important elements in the production process. Vessel size reflects fishing capacity and constrains the areas and seasons of operation. Smaller vessels below approximately 30 gross registered tons (GRT) are generally limited to inshore day trips during favorable seasons. Vessels of about 45 to 60 GRT make either single or multiday trips in nearshore waters, depending upon the season and expected prices and resource abundance. Vessels over 60 GRT are less subject to seasonality, fish year round, can fish offshore, and make multiday trips.

Crew size can vary, although as in all production processes, only within a range. Vessels of certain sizes and designs have minimum crew requirements. Institutional factors such as tradition, family ties, ethnicity, or the New Bedford union (Teamsters Local #59) can make changes in crew size difficult. Nevertheless, crew sizes can, and do, change according to economic conditions (Moss and Terkla, 1985).

A typical fishing trip might consist of steaming to the desired initial fishing ground, where the otter trawl net is released and towed for several hours. The harvest is then hauled in, and the fish sorted, gutted, and packed in ice. Captains can alter the level and composition of catch by selection of net type, mesh size, speed and depth of tow, fishing grounds, and so forth. Changes in species composition occur with changes in expected relative output and factor prices, biological abundance, and seasonality. After return to port, proceeds from sale of the catch are apportioned among vessel, crew, and trip expenses by the lay system. In this system various trip or operating costs, such as fuel, food, and ice, are first subtracted from the gross revenue, and this net trip revenue is then divided among captain, crew, and owner of the vessel. The particular formula for allocating shares varies by port, and to a lesser extent, by vessel.

3. Empirical specification

■ Bioeconomic models traditionally form the conceptual basis for regulation of multispecies fishing industries. The basic model consists of a single aggregate input, fishing effort, and either an aggregate output, total catch, or a separate production process and model for each species (Clark and Munro, 1980). Simplified and deterministic population dynamics are specified, which relate gross weight of the biomass to growth, mortality, and environmental parameters. The aggregate production function relates total industry catch to industry effort and resource abundance in a restrictive functional form, almost invariably the Cobb-Douglas structure. The basic static model then combines the population dynamics and fishery production function to give steady-state optimal levels of catch, effort, and abundance. Regulatory agencies compare the unregulated, free-entry levels to target solutions, and manage the control variable, effort, accordingly. Capital-theoretic or dynamic models further provide optimal time paths of catch, effort, and abundance.

The theory of duality at the level of the firm offers an attractive alternative to the bioeconomic approach. While the dual framework does not focus on steady-state levels of

the variables, it offers the more immediate and detailed knowledge of the individual firm's technology and costs required for practical regulation. The approach obviates the conceptual problem of managing industry abstractions, catch and effort, and instead offers specific empirical knowledge to regulate the individual inputs and outputs comprising these variables. Public regulation can then be consistent with the technological and cost conditions facing firms. The procedure also accords better with the limited regulatory power and uncertain biological information often encountered by management agencies, and it does not rely upon the questionable existence of an aggregate input and an aggregate production function.

The brief survey of the New England otter trawl industry suggests a number of guidelines for modelling the firm's production technology by the dual approach. First and foremost, the presence of multiple species implies a multiproduct technology, which should include as outputs the most important species: cod, haddock, and yellowtail and other flounders. Second, during 1980 and 1981, the time period of concern, outputs can largely be considered as freely variable and endogenously determined.³ Third, the large number of vessels in the industry, homogeneous products, and minimal vertical and horizontal integration assure exogenously determined output prices. Fourth, although the labor payments are based on a share system, the proper economic valuation is the opportunity cost of labor.⁴ This approach also provides an exogenous wage rate for the model. Fifth, crew sizes are variable, although probably only within a somewhat restricted range, and more variable in larger vessels than in smaller ones. Sixth, along with labor, fuel and capital (in the form of the vessel, gear, and equipment) are organized to produce the multiple products.

Fishing firms may thus be regarded as multiproduct firms producing a vector of endogenous outputs from a vector of endogenous inputs. This suggests that the multiproduct profit function is the appropriate dual representation of the firm's production technology. Finally, the area in which a firm operated can affect the production technology through port effects on prices and the spatial distribution of fish stocks. To account for these effects, three area dummy variables are included: one each for New Bedford, Rhode Island, and Maine. The intercept includes Gloucester, Boston, Provincetown, and the remaining Massachusetts ports other than New Bedford.

A choice must also be made between using a restricted or a full static equilibrium representation of technology. The lumpiness and long life of fishing vessels suggest a restricted model with capital as a fixed factor. Alternatively, a full static equilibrium model may be more suitable, since used and new vessel markets, vessel leasings, and deliberate vessel sinkings for insurance are important aspects of the capital market. Moreover, otter trawlers are mobile and can easily switch gear, location, and targeted species. Squires (forthcoming) finds full static equilibrium to be the appropriate specification after application of Kulatilaka's (1985) parametric test.

I therefore use a full static equilibrium multiproduct profit function with the results conditional on existing stock levels of the species. A translog profit function is specified as a second-order Taylor series approximation:

$$\ln H = A_0 + A_T T + \sum_{k \in F} A_k R_k + \sum_{i \in F} A_i \ln P_i + \sum_{i \in F} \sum_{j \in F} A_{ij} \ln P_i \ln P_j \\ + \sum_{i \in F} A_{iT} T \ln P_i + \sum_{i \in F} \sum_{k \in F} A_{ik} R_k \ln P_i, \quad (1)$$

³ Even if limits on the catch of each trip were to some degree binding in 1980, the use of annual data suggests that as fishermen make more frequent and shorter trips, outputs are still variable, but at the cost of technical inefficiency. See also footnote 2.

⁴ Clark and Munro (1980) adopt the opportunity-cost approach in their model of fisheries production. This procedure is also commonly followed in studies of agriculture in which family labor is involved (Lopez, 1984). The approach is also fundamental to deriving capital service prices and the concept of normal profit.

where H is economic profit (total revenue less the costs of fuel and oil, capital services, and total opportunity cost of labor), P is an $F \times 1$ vector of strictly positive species prices (M of them) and input prices (N of them), T is an annual dummy variable for 1981, and R_k is the k th of the three area dummy variables.

I obtain the revenue and cost share equations by applying Hotelling's lemma:

$$\frac{\partial \ln H}{\partial \ln P_i} = \frac{P_i Y_i}{H} = A_i + A_{iT}T + \sum_{k \in 3} A_{ik}R_k + \sum_{j \in F} A_{ij} \ln P_j, \quad \forall i \in F, \quad (2)$$

where Y_i is the quantity of the i th input or output. These shares are positive for outputs and negative for inputs. Without loss of generality, symmetry is imposed by $A_{ij} = A_{ji}$ for $i \neq j$ in (1) and (2). Equality between the parameters of the profit and share equations is maintained. Linear homogeneity in prices is imposed on the profit function by: $\sum_{i \in F} A_i = 1$, $\sum_{i \in F} A_{iT} = \sum_{i \in F} A_{ik} = \sum_{i \in F} A_{ij} = \sum_{j \in F} A_{ij} = \sum_{i \in F} \sum_{j \in F} A_{ij} = 0$.

The most disaggregated version of (1) and (2) specifies five outputs: cod, haddock, yellowtail flounder, other flounders, and a residual (all others) and three inputs: capital services, labor (including the captain), and energy (fuel and oil) consumption. Resource abundance is specified as a technological constraint since it is beyond the control of any individual firm but nevertheless affects the production environment within which the firm operates. Changes in resource abundance may then be viewed as shifts in the production technology that relates the generation of outputs from inputs (McFadden, 1978). These changes are represented by the 1981 dummy variable.

□ **The data.** The balanced panel data set consists of annual observations for 2 years, 1980–1981, on 42 full-time otter trawlers, each of which was absent from port for at least 85 days in each year. Home ports for the vessel and crew in each year are assigned by a plurality of days absent from port. All of the major New England ports are represented, as well as a number of minor ones such as Newport, Rhode Island, and Sandwich and Plymouth, Massachusetts.

The data set includes the more productive vessels of the full-time near- and offshore otter trawl fleet. This sector accounts for over 80% of the entire fleet's landings and is therefore the most important for regulation. The mean sample vessel is 120 GRT, has a crew size of 5, and was built in 1972. In contrast, the entire fleet's mean vessel is 70 GRT with 3 crew members. The mean sample vessel's days absent from port is 167, with a range of 85 to 249, and the vessel makes an average of 57 trips per year of 3 days' duration (with a range of 1 to 13 days). The sample vessels are typically larger and spend more time fishing than the mean fleet vessel.

All of the revenue, landings, and vessel and trip characteristics data are from the National Marine Fisheries Service Weighout File. Implicit exvessel species prices are formed by dividing total revenue by total pounds landed. Fuel and oil costs are from federal income tax returns. Most vessel acquisition prices (including hull, gear, equipment, and engine) are exact and compiled from receipts; the remainder are from federal tax returns. Both new and used vessels are included, although the majority are new vessels. Only those vessels purchased between late 1976 and 1979 are included, to eliminate effects of vintage and structural changes in the industry that resulted from the Magnuson Act. Any new equipment and gear purchased in 1980 for use in 1981 are included. Because most of the sample consists of vessels participating in National Maritime Fisheries Service loan guarantee or capital construction fund programs, the vessels tend to be newer and more successful than most of the fleet. Most data are confidential.

The opportunity cost of labor per crew member is an exogenous measure of returns to labor and food costs per person. Since little reliable empirical evidence is available on fishermen's alternative employment possibilities, it is assumed only that fishermen will work

in the major port towns, which are predominantly industrial and blue collar. The opportunity cost of labor per crew member is a Divisia index of the opportunity costs of the crew (mean annual income of total manufacturing), the mechanic (mean annual income of maintenance mechanic, machinery), and captain (annual income 20% higher than an ordinary seaman's). These indexes vary by both crew size and port. To derive the index, crew members are assigned to one of five New England coastal manufacturing cities (Portland, Gloucester, Boston, New Bedford, and Providence) on the basis of the geographical proximity of their home ports. Labor cost data are from the U.S. Department of Labor, Bureau of Labor Statistics, and from comparable state agencies.

Energy prices are cash prices for number two diesel fuel from marine fuel docks of the major ports, and vessels from minor ports are assumed to face the energy prices of the closest major ports. Energy costs include sales taxes. The capital services price comprises the opportunity cost of capital and depreciation. All values are deflated by the GNP implicit price index.

The profit function (1) has an additive disturbance term owing to approximation error, while the revenue and cost share equations (2) have additive disturbances from errors in optimization (Burgess, 1975). Disturbances are also likely to arise from the stochastic nature of fishing. Since the share equations sum to unity, the energy consumption equation is omitted and its parameters are identified through the linear homogeneity and symmetry constraints. I estimate the system (1) and (2) jointly by maximum likelihood.

4. Public regulation and the structure of production

■ The structure of production has several implications for efforts to regulate multiproduct production by managing the levels of inputs and outputs. The production constraints imposed can be either primal, such as output quotas, or dual, such as an output tax or a fee on the number of production units or firms in an industry. The two types of constraint are equivalent at the level of formal analysis in a static, full-information, deterministic framework (Weitzman, 1974).

□ **Aggregation.** The appropriate level of aggregation of inputs and outputs carries with it important implications for public regulation. At the highest level of aggregation, only a single composite output and input exist. Multispecies bioeconomic models traditionally maintain this level of aggregation, where the composite input is called fishing effort. This level of aggregation requires separability between inputs and outputs, and it implies that the marginal rates of substitution between factor pairs are independent of the composition of catch, while the marginal rates of transformation between species pairs are independent of the composition of inputs. Conceptually, only the levels of the catch and effort require regulation, and regulation of the input (species) mix does not adversely affect the optimal product (factor) combinations. Considerable flexibility is thus afforded to regulators. The econometric restriction needed to test for input-output separability is that there is no interaction between inputs and outputs: $A_{ij} = 0$, $i \neq j$, $i \in M$, $j \in N$. The likelihood ratio test is employed to test this and all other restrictions.⁵

Lower levels of aggregation, and thus separability, allow more precise targeting of regulations. Output (input) separability implies a single product (factor) and independence of optimal product (factor) combinations from the composition of inputs (outputs). Weak separability among only a subset of inputs or outputs may also exist. It implies that the marginal rates of substitution or transformation between variables of a subset are independent

⁵ The likelihood ratio L is the ratio of the restricted to the unrestricted maximum value of the likelihood function. The test statistic formed by $-2 \ln L$ is asymptotically distributed as a chi-square with degrees of freedom equal to the number of independent restrictions. A significance level of 1% is adopted.

of the mix of other variables. This allows separate regulation of the subset's components without affecting the optimal mixes of the remaining outputs and inputs. Tests for weak separability are applied to the two most economically important species groupings, cod and haddock to form the aggregate roundfish, and yellowtail and other flounders to form flatfish. Weak separability at the point of approximation of some partition I of outputs requires that $A_j A_{ik} - A_i A_{jk} = 0$, $i \neq j \neq k$, $\forall i, j \in I$, $k \notin I$ (Denny and Fuss, 1977).

If the profit function is weakly separable over a subset of its outputs, such as cod and haddock, the firm's optimization procedure can be treated as a two-stage process. The optimal combination of outputs within the subgroup is selected first, followed by the choice of the appropriate levels of the aggregate for this subgroup and of the other outputs and inputs. Homotheticity of the profit function in this product group then allows consistent aggregation within the subgroup so that the product of the price and quantity indexes for it equals its total value. With the translog form, the restriction for homotheticity of a subset I of outputs is: $\sum_{j \in I} A_{ij} = 0$, $\forall i \in I$.

The two-stage optimization procedure may be applied by using the translog unit revenue function as a price aggregator function (Fuss, 1977). The translog price index provides a Tornquist discrete approximation to the Divisia index and is written as:

$$\ln P_I = B_0 + \sum_{a \in I} B_{aT} T \ln P_a + \sum_{a \in I} \sum_{k \in 3} B_{ak} R_k \ln P_a + \sum_{a \in I} \sum_{b \in I} B_{ab} \ln P_a \ln P_b, \quad (3)$$

where linear homogeneity and symmetry are imposed. Since P_I is an unobservable variable, equation (3) cannot be estimated directly. Instead, a set of revenue share equations is derived by using Hotelling's lemma and estimated by maximum likelihood:

$$U_a = B_a + B_{aT} + \sum_{k \in 3} B_{ak} R_k + \sum_{b \in I} B_{ab} \ln P_b, \quad \forall a \in I, \quad (4)$$

where U_a is the revenue share of the a th output in the set I for which the aggregate has been formed. Estimated parameter values from (4) are then inserted in (3) to obtain an estimate of $\ln P_I$, which is then used in the estimation of the profit function (1) and share equations (2) (Fuss, 1977).

□ **Jointness.** Public regulation of production in multiproduct industries is afforded additional precision and flexibility if there exist separate production processes for outputs, that is, if production is nonjoint in inputs. The output of any single process then depends only on the inputs used in that process and not on the level of inputs or output(s) in any other production process. Each production process can be separately regulated without affecting production of the other processes because there are no technological or cost tradeoffs between the output of one activity and that of another. The existence of a production process for each output i is tested with the translog form at the point of approximation by $A_{ij} = -A_i A_j$, $i \neq j$, $i, j \in M$ (Denny and Pinto, 1978).

The results of this test for nonjointness in inputs will also have important implications for the specification of the fishery production function in multispecies bioeconomic models. These models traditionally assume either nonjoint production (a separate production function for each species) or input-output separability with joint production (a single output and input, and all inputs used to produce all outputs).

□ **Transformation and substitution possibilities.** By restricting individual inputs and outputs, public regulation may induce inefficiency and unexpected results. Input regulation can limit the use of certain inputs in production or it can limit entry into an industry. Effective regulation of inputs may then induce unanticipated expansion of unregulated inputs and cause inefficient production (DeVany *et al.*, 1982). Market contestability or free

entry might also be reduced if regulation limits the mobility of capital and the recoverability of fixed costs. Output levels can similarly be constrained, and thus lead to unanticipated transformations and inefficiency.

The Marshallian elasticities of factor demand and product supply obtained from the profit function indicate substitute or complementary relationships among inputs and outputs and therefore the possibility of unanticipated expansions or contractions of factors and products when regulation is imposed. These elasticities include both expansion effects and pure substitution effects. With the translog form, the elasticities' formulas are: $V_{ii} = (A_{ii} + U_i^2 - U_i)/U_i \forall i \in M, N$ and $V_{ij} = (A_{ij} + U_i U_j)/U_i, \forall i, j \in M, N$, where U_i is the i th fitted share at the sample arithmetic mean, and $U_i > 0$ for outputs and $U_i < 0$ for inputs.

When the two-stage optimization procedure is applied to a group of outputs, two elasticities can be computed for any two outputs a and b (e.g., cod and haddock) aggregated into I (roundfish). The gross price elasticity E_{ab}^* is conditional on the fixed aggregate I , while the net price elasticity E_{ab} allows the aggregate I to be endogenous. Outputs could be gross complements in the first stage, yet net substitutes in the second. The relationship between the gross and net price elasticities is $E_{ab} = E_{ab}^* + U_b V_{II}$, $a, b \in I$, where U_b is the fitted revenue share of output b in the aggregator function for I (equation 4) and V_{II} is the Marshallian own-price elasticity of I (Fuss, 1977).

□ **Multiproduct cost structure.** The firm's structure of costs provides further information that is useful for public regulation that aims to promote efficient production and multiproduct industry structure. The measure of multiproduct (ray) returns to scale offers an indication of the efficiency of the scale of production for the existing product mix and level of resource abundance. Regulation of production can alter the overall scale of production by affecting the levels and mixes of outputs and inputs and, in natural resource industries, by altering the mix and level of resource availability. The degree of overall scale economies at the point of approximation for the translog form is calculated by $S_M = \sum_{j \in N} U_j / \sum_{i \in M} U_i$ (Weaver, 1983).

Product-specific economies of scale measure the change in costs through variations in the output of one product while holding the quantities of other products constant. These measures can indicate whether public regulation might encourage expansion in the scale of production of individual products and whether specialized firms producing only a single product are likely. They can also alert managers to a natural resource that may suffer excessive depletion as firms expand their production to enjoy cost savings. Although product-specific economies of scale cannot be directly measured by the translog profit function, sufficient information is obtained by examining the structure of incremental marginal costs (Baumol, Panzar, and Willig, 1982). The measure for product i at the point of approximation is $S_i = (A_{ii} + A_i^2 - A_i)^{-1}$. An estimated value less (greater) than zero implies decreasing (increasing) product-specific returns to scale for product i .

Although economies may be associated with the level of output, economies may also be associated with the composition of output. Public regulatory agencies can use knowledge about such economies to assess the relative efficiencies of different product combinations and to design their policies accordingly. For example, if joint harvesting of several fish species results in cost savings, then regulating one of the species might increase harvesting costs of the other species. Economies of scope measure these effects of joint production upon costs in which production that jointly uses inputs costs less than independent production of several products. The profit function cannot directly measure overall economies of scope, but weak cost complementarity between product pairs provides a sufficient condition for such economies to exist in the long run (Baumol, Panzar, and Willig, 1982). The condition for pairwise weak cost complementarity at the point of approximation provides

a nonstatistical test of economies of scope, and with the translog form, this condition is $S_{ij} = (A_{ij} + A_i A_j)^{-1} < 0$, $i \neq j$, $i, j \in M$.⁶

5. Empirical results and implications for public policy

■ The values of the estimated parameters of the disaggregated model are not reported, but they are available from the author upon request. The generalized R^2 is .99, and is calculated as $1 - \exp[2(L_1 - L_2)/N]$, where $L_1(L_2)$ is the maximum value of the log-likelihood function when all slope coefficients are zero (unconstrained), and N is the total number of observations. The ordinary least squares R^2 's of the individual share equations range from .30 to .53, and the ordinary least squares R^2 of the profit function is .88. The predicted share equations are positive (negative) for outputs (inputs) over all observations, which indicates that monotonicity is satisfied.

The profit function is not convex at 81% of the sample points. Parameter estimates and tests may be inconsistent with expectations of the competitive model, although this is not a statistical test. Convexity is implied by the assumption of profit maximization, but a test of convexity cannot be interpreted as a strict test of this assumption because convexity may be violated for a number of other reasons. For example, Wales (1977) shows that estimates of a flexible functional form may violate convexity even if the data come from a well-behaved technology. Inconsistent aggregation, such as the linear aggregation over 50 different, minor species groups to form the all others species aggregate, can also contribute to the failure to obtain convexity. Finally, although eliminating statistically insignificant parameters from the model can lead to convexity, one would be imposing an unknown structure upon the results.

The translog form was selected as in Lopez (1985). A problem arose for 16 of the 420 total output observations because a zero output was encountered, and, of course, the translog form is not well defined when an output level is zero. The Box-Cox transformation ostensibly provides one solution to this problem, but this form imposes input-output separability and additive separability for linear profit terms (Lopez, 1985) and assumes nonnormal disturbances before transformation. The recently proposed procedure of Lee and Pitt (1986), using virtual prices, is not yet computationally feasible with the number of variables of this study. The solution adopted here was to estimate the function at an arbitrarily small level of output prices, .01. Robustness of the estimated results was assessed by reestimating the model with a range of small product price levels, .10 and .001 and by including a dummy variable when a zero output appears. The log-likelihood value changes by .04% with the dummy variable approach, by 2.6% with .10 price values, and by .6% with .001 price values. Parameter estimates are generally robust except for the .10 case, in which some of the haddock and yellowtail flounder values (where all the zero outputs occur) are most affected. The overall qualitative results of the model are likely to be robust to the value selected to represent zero output prices.

The empirical results provide only limited support for the traditional bioeconomic model. A detailed report of the hypothesis tests is given in the Appendix. I find evidence for jointness in inputs or a single production process, but support is not provided for the existence of a composite index of outputs (total catch) and inputs (fishing effort) or for a Cobb-Douglas functional form. Weak separability is found for roundfish (cod and haddock) and flatfish (yellowtail and other flounders), but a consistent translog aggregate can be formed by the two-stage optimization procedure only for roundfish. Fishermen thus separately

⁶ Lopez (1984) and Sakai (1974) show that $\partial^2 C / \partial Y_i \partial Y_j = [\partial^2 H / \partial P_i \partial P_j]^{-1}$ and $\partial^2 C / \partial Y_i^2 = [\partial^2 H / \partial P_i^2]^{-1}$, $i, j \in M$. By Hotelling's lemma and marginal cost pricing, $[\partial^2 H / \partial P_i \partial P_j]^{-1} = \{\partial Y_i / \partial (\partial C / \partial Y_j)\}^{-1}$, which provides the definition of weak cost complementarity between products i and j . The extension to incremental marginal costs is straightforward.

optimize revenue and species mix for roundfish and flatfish before beginning the general profit maximization problem.

The profit function is reestimated with a translog aggregate for roundfish in the form of equation (3). Table 1 provides the parameter estimates for the translog roundfish unit revenue function. Table 2 reports the profit function's parameter estimates.

The estimated structure of production does not provide encouragement for a program of straightforward, simple regulation of production. A multiproduct production technology without separability between inputs and outputs precludes simply regulating the levels of total catch and fishing effort. Instead, individual outputs or inputs must be regulated. Optimal output and input mixes can be adversely affected by regulatory constraints because input and output allocation decisions are not independent. The separability of roundfish and flatfish does allow regulation of their individual components without distorting the optimal output and input proportions. Joint-in-inputs production further narrows the regulatory options by precluding separate regulation of individual harvesting processes: the problem of technological and cost interdependence with joint production must be addressed.

□ **Technological interdependence.** The technological tradeoffs among inputs and outputs with joint harvesting are measured by the Marshallian elasticities reported in Table 3.⁷ Not

TABLE 1 Parameter Estimates of Roundfish
Unit Revenue Function*

Prices and Other Exogenous Variables	Revenue Shares	
	Cod	Haddock ^a
Intercept	.631 (.039)	.369 (.039)
1981 Dummy	-.019 (.040)	.019 (.040)
New Bedford Dummy	.198 (.051)	-.198 (.051)
Rhode Island Dummy	.291 (.057)	-.291 (.057)
Maine Dummy	.171 (.055)	-.171 (.055)
Cod Price	.057 (.022)	-.057 (.022)
Haddock Price	-.057 (.022)	.057 (.022)
R^2	.58	
S.E.	.173	

* Standard errors in parentheses. Translog unit revenue function with symmetry and linear homogeneity directly imposed.

^a Parameter estimates are derived from the constraints for linear homogeneity and symmetry. Linearized standard errors in parentheses.

⁷ Again, these elasticities include both expansion and transformation effects. Standard errors of the elasticities are computed as square roots of $\text{var}(A_{ij})/U_i^2$ and $\text{var}(A_{ij})/U_j^2$. The fitted values of the shares are treated as non-stochastic.

shown there are the net cross-price elasticities for cod and haddock, the components of roundfish, which are .41 and .66, indicating inelastic net complementarity. The results in Table 3 indicate that the landings levels for different species can be reduced by regulating only a limited number of species because of the widespread Marshallian complementarity among outputs. Expansions in the overall levels of landings of unregulated species are not a serious problem since only limited Marshallian species substitution exists.

Substitution of unregulated species for the regulated species may still occur although the absolute level of each species declines. Pressures that are greater than anticipated may then be placed upon the resource stock, catches of even regulated species could surpass the established quotas, and inefficient product proportions are still possible. Regulators might respond by additional management measures, which increase the complexity of regulations and create further uncertainty in the production environment. Allen elasticities of product transformation measuring the pure transformation possibilities are presented in Table 4.⁸

TABLE 2 Parameter Estimates of Translog Profit Function*

Prices and Other Exogenous Variables	Product Shares				Factor Shares			Profit Function
	Roundfish	Yellowtail Flounder	Other Flounders	All Others	Capital	Labor	Fuel ^a	
Intercept	15.267 (2.793)	-.706 (1.058)	16.818 (2.014)	7.449 (1.792)	-9.317 (.739)	-9.763 (1.195)	-18.747 (2.608)	130.965 (10.370)
1981 Dummy	-.525 (.159)	.010 (.044)	-.384 (.145)	.205 (.107)	.248 (.067)	.233 (.118)	.212 (.075)	-5.666 (1.893)
New Bedford Dummy	.090 (.266)	.271 (.083)	.264 (.223)	-.318 (.186)	-.078 (.122)	-.182 (.207)	-.048 (.128)	2.518 (3.509)
Rhode Island Dummy	-.927 (.236)	.358 (.090)	-.351 (.237)	.030 (.146)	.052 (.110)	.501 (.181)	.337 (.039)	-6.498 (2.905)
Maine Dummy	-.948 (.297)	.089 (.074)	-.353 (.249)	.359 (.223)	.262 (.123)	.300 (.227)	.291 (.142)	-6.261 (3.614)
Roundfish	-.027 (.173)	.069 (.089)	1.347 (.269)	.036 (.138)	-.463 (.098)	-.782 (.201)	-.181 (.221)	
Yellowtail Flounders		.043 (.017)	-.124 (.086)	-.026 (.041)	.018 (.035)	.059 (.069)	-.039 (.054)	
Other Flounders			.474 (.160)	.596 (.140)	-.519 (.069)	-.841 (.150)	-.934 (.158)	
All Others				.163 (.040)	-.195 (.064)	-.441 (.101)	-.133 (.114)	
Capital					.105 (.009)	.682 (.064)	.372 (.057)	
Labor						-.032 (.063)	1.356 (.233)	
Fuel							-.442 (.879)	

* Standard errors in parentheses. Symmetry and linear homogeneity in prices directly imposed.

^a Parameter estimates derived from symmetry and linear homogeneity constraints. Linearized standard errors in parentheses.

⁸ Marshallian cross price product supply elasticities (ϵ_{ij}^M) include both expansion and pure substitution effects since factor levels are allowed to change with changes in product prices (Sakai, 1974). A decrease in a product price

TABLE 3 Marshallian Product Supply and Factor Demand Elasticities*

Price	Roundfish	Yellowtail Flounder	Other Flounder	All Others	Capital	Labor	Fuel
Roundfish	.31 ^a (.13)	2.03 ^a (.90)	3.44 ^a (.42)	1.45 ^a (.47)	2.28 ^a (.21)	3.13 ^a (.46)	1.74 ^a (.51)
Yellowtail Flounder	.15 ^a (.07)	-.47 ^a (.17)	-.10 (.13)	.01 (.14)	.06 (.07)	-.04 (.16)	(.19) (.12)
Other Flounder	1.66 ^a (.20)	-.62 (.87)	.38 (.26)	2.68 ^a (.48)	1.71 ^a (.14)	2.58 ^a (.34)	2.78 ^a (.36)
All Others	.32 ^a (.10)	.03 (.42)	1.23 ^a (.22)	-.15 (.14)	.69 ^a (.13)	1.31 ^a (.23)	.60 ^a (.26)
Capital	-.84 ^a (.08)	-.30 (.36)	-1.30 ^a (.11)	-1.15 ^a (.22)	-1.70 ^a (.02)	-2.06 ^a (.15)	-1.34 ^a (.13)
Labor	-1.02 ^a (.15)	.16 (.70)	-1.75 ^a (.24)	-1.94 ^a (.35)	-1.84 ^a (.13)	-1.36 ^a (.15)	-3.55 ^a (.54)
Fuel	-.587 ^a (.17)	-.83 (.54)	-1.90 ^a (.25)	-.89 ^a (.39)	-1.20 ^a (.01)	-3.57 ^a (.13)	-.42 (2.01)

* Elasticities evaluated at 1980 mean levels for Gloucester, Boston, and other Massachusetts ports except New Bedford. Linearized standard errors in parentheses.

^a Elasticities significant at 1%.

The mixed pattern of complementarity and substitutability one sees in Table 4 indicates that unanticipated catches of both regulated and unregulated species are possible in this joint-harvesting fishery. Catches exceeding the quota are discarded (or illegally landed). Individual species regulation thus does not necessarily reduce catches to the quota levels, and such regulation can be a counterproductive means to rebuild multispecies resource stocks. In fact, the otter trawl industry experienced just such effects when the Fishery Council attempted to regulate cod, haddock, and yellowtail as individual, nonjoint production processes.

TABLE 4 Allen Elasticities of Product Transformation*

	Yellowtail Flounder	Other Flounder	All Others
Roundfish	1.15	1.14	-0.09
Yellowtail Flounders		-1.42	-0.71
Other Flounders			1.41

* Elasticities evaluated at 1980 mean levels for all Massachusetts ports except New Bedford.

might induce movement along a given product transformation frontier (pure substitution effect) and changes in all the inputs along the new expansion path (expansion effect). Marshallian cross price factor demand elasticities similarly include expansion and substitution effects, and all inputs can be Marshallian complements (Sakai, 1974). Hicksian or compensated product supply elasticities (R_{ij}) hold input levels constant and provide pure substitution effects among product pairs along a transformation frontier. They are calculated from Marshallian elasticities by $[R_{ij}] = [V_{ij}] - [V_{ik}][V_{kl}]^{-1}[V_{kj}]$, where i, j are products and k, l are inputs (Lopez, 1984). Similarly, Hicksian or compensated factor demand elasticities hold output levels constant and measure pure substitution effects among input pairs along an isoquant. They are calculated by $[R_{kl}] = [V_{kl}] - [V_{ki}][V_{ij}]^{-1}[V_{il}]$. Allen elasticities of product transformation and factor substitution are calculated from the Hicksian elasticities by $AET_{ij} = R_{ij}/U_j$ and $AES_{kl} = R_{kl}/U_l$.

Individual species regulation can generate economic inefficiency not only by the catch discards it causes but also by inducing nonoptimal input and output mixes. Economic inefficiency can also occur if trip limits are imposed and fishermen make more frequent trips, thereby increasing running time and fuel consumption. Pressures on the more accessible resource stocks also increase, which reduces catch productivity and increases costs. Landings taxes may also induce inefficient output proportions as the relative exvessel species prices are altered. Inefficient production can also be generated if fishermen increase input usage to maintain some overall minimum level of total revenue (perhaps to make vessel payments) when higher-valued species are regulated.

The alternative of regulating individual inputs is more effective and consistent with the structure of production. Because of the extensive Marshallian complementarity among inputs reported in Table 3, the levels of all inputs will decline with the restriction of any single input. The most readily monitored and managed input can be targeted for regulation. In turn, catch levels and pressures upon the resource stock will decline as indicated by the significant production elasticities between inputs and outputs of Table 3. Yet, even though the absolute level of each input declines, fishermen may still substitute unregulated for regulated inputs. Allen elasticities of substitution measuring the pure substitution possibilities are reported in Table 5. Both substitutability and complementarity among factor pairs are identified. Since unanticipated factor substitution is likely, more than one input can be regulated, thereby precluding inefficient factor and product proportions and keeping pressure on catches and resource stocks closer to targeted levels. Economic inefficiency from catch discards is eliminated. Input regulation is also easier to enforce and less costly than catch management since inputs can be monitored dockside rather than on the open sea. The composition of catch can even be controlled by regulatory agencies through minimum mesh sizes and other controls on gear selectivity.

A program regulating inputs might restrict entry to the industry by limiting the number of vessels. Unexpected expansions in productive capacity may then occur as fishermen attempt to appropriate any increases in economic rents by expanding harvesting capacity through larger vessels, engines, gear, and nets and by installing additional electronic equipment. Declines in economic rents and socially inefficient resource depletion are then likely. The elasticity of capital demand with respect to its own price, identified in Table 3, indicates that changes in capitalization are not difficult to make.⁹ Crew sizes may also increase because labor is a complement to capital. Provisions against capacity expansion are therefore important to any limited-entry program.

Achieving targeted goals does not require particularly strong constraints because of the generally elastic substitution possibilities. In this sense direct quantity controls are as likely

TABLE 5 Allen Elasticities of Factor Substitution*

	Labor	Fuel
Capital	-.45	.47
Labor		2.69

* Elasticities evaluated at 1980 mean levels for all Massachusetts ports except New Bedford.

⁹ This result is also consistent with the finding of full static equilibrium reported earlier. In addition, the elastic own-price factor demands indicate that should output restrictions be tied to some measure of productive capacity, such as crew or vessel size, sizeable expansions of this input are likely. This happened in New England when individual species quotas were directly tied to crew sizes and crew sizes subsequently expanded.

to realize management goals as are indirect controls through taxes or fees. They also directly address the problems, are usually more amenable to change, and are under the control of a single Fishery Council rather than different state legislatures.

□ **Multiproduct cost structure.** The estimated structure of multiproduct costs is reported in Table 6. Economies of scope exist only between yellowtail flounder and each of the other sets of species. Yellowtail flounder is a pivotal species in the industry because cost savings accrue to vessels harvesting yellowtail with any of the other species. The estimated incremental marginal costs imply decreasing product-specific returns to scale for roundfish, other flounders, and all others. Declining product-specific marginal and average cost curves and increasing product-specific returns to scale are indicated for yellowtail flounder. The implied declining product-specific yellowtail supply curve may explain the significant negative own-price supply elasticity in Table 3 and some of the apparent difficulties in attaining convexity. Declining yellowtail stocks that are placed under excessive harvesting pressure can cause excess yellowtail harvesting capacity, and therefore the declining product-specific cost and supply curves.

The strong cost incentives to harvesting yellowtail because of economies of scope and the increasing product-specific returns to scale make the yellowtail resource stock vulnerable to intensive harvesting. Nonetheless, specialized yellowtail firms are unlikely because of the economies of scope realized by jointly harvesting yellowtail with other species.

The estimates of multiproduct returns to scale are .58 for 1980 and .62 for 1981. Multiproduct returns to scale are decreasing, and neither cost nor profit advantages accrue from harvesting more fish in fixed proportions while holding prices and resource abundance constant. As the scale of production expands for a given level of resource abundance, vessels fish in more marginal grounds and in more inclement weather, increase search time, and so forth. Firms should realize cost savings as the resource stocks recover under regulation.¹⁰

The multiproduct cost structure provides additional impetus to individual input regulation. Most output regulations affect yellowtail flounder because of the technological and cost interdependencies of joint harvesting. Firms then cannot fully enjoy economies of scope and product-specific returns to scale for yellowtail. Harvesting costs, economic efficiency, and possibly even the degree of firm diversification are affected throughout the industry. In contrast, input regulation does not affect economies of scope, although some firms' costs may increase if they cannot realize increasing product-specific returns to scale for yellowtail. Public regulation, even limiting the number of vessels, should also have minimal concern for a noncompetitive industry structure, since few cost incentives are present for firm amalgamation or a larger scale of production realized by fewer vessels.

TABLE 6 Multiproduct Cost Structure*

	Measure of Weak Cost Complementarity			Incremental Marginal Costs
	Roundfish	Yellowtail Flounder	Other Flounders	
Roundfish				.004
Yellowtail Flounder	-.093			-2.183
Other Flounders	.004	-.083		.004
All Others	.009	-.189	.008	.018

* Evaluated at 1980 mean levels for all Massachusetts ports except New Bedford.

¹⁰ As stocks recover, the transformation frontier should shift out, away from the origin, and increasing overall returns to scale are possible. Kirkley (1986) finds increasing overall returns to scale when estimating a multiproduct revenue function with resource abundance assessment levels specified as a technological constraint.

The actual choice of policy and instruments depends upon considerations beyond the scope of this study. To the extent possible, however, the regulatory program should be consistent with the structures of production and costs, and equally important, it should be readily accommodating to change.

6. Concluding remarks

■ This study finds that public regulation of multispecies fishing industries may previously have been inappropriately designed. Traditionally, the regulatory task has been conceived as one of either managing total industry catch and aggregate industry input, fishing effort, or *ad hoc* regulation of individual species as nonjoint production processes. The traditional bioeconomic model has formed the conceptual basis of this approach. Multispecies fisheries management can instead be approached as a process of regulating the production of individual multiproduct firms. In New England regulation consistent with this approach would directly regulate more than one input. Inefficient product and factor proportions, catch discards, and an inefficient cost structure would be prevented while reducing productive capacity and catch levels. In turn, resource stocks should recover and economic rents increase. Finally, only limited support is provided for the traditional bioeconomic model in the New England fishery studied.

Appendix

■ The hypothesis that production is nonjoint in inputs is rejected, since the likelihood ratio test statistic is 52.9 and the 1% critical value is 23.2. This implies that separate harvesting processes do not exist for the five species. (An anonymous reviewer suggests that trip limits, if effective, would make nonjoint production virtually impossible.) Input-output separability is rejected, since the test statistic is 116.6 and the 1% critical value is 30.6. Rejection of input-output separability with the translog form also implies rejection of a Cobb-Douglas form (Denny and Fuss, 1977). Weak separability of all outputs and inputs are each individually rejected because the chi-square statistics are 30.9 and 28.2, while the 1% critical values are 18.5 and 15.1 with 7 and 5 independent restrictions for outputs and inputs, respectively. These separability tests imply that consistent aggregates for total output (catch) and all inputs (fishing effort) and the traditional Cobb-Douglas fishery production function of bioeconomic models do not exist.

Weak separability is not rejected for either roundfish or flatfish, while weak homothetic separability is not rejected only for roundfish. The test statistics for weak separability of the two aggregates are 14.9 and 12.3, while the 1% critical value is 15.1. The test statistics for homotheticity are 4.5 and 21.5, while the 1% critical value is 9.2. A consistent aggregate can be formed only for roundfish.

The null hypothesis that the area dummy variables are unimportant is rejected since the test statistic is 158.7, while the 1% critical value is 38.9 for 21 independent restrictions.

References

- BAUMOL, W., PANZAR, J., AND WILLIG, R. *Contestable Markets and the Theory of Industry Structure*. New York: Harcourt-Brace-Jovanovich, 1982.
- BURGESS, D.F. "Duality Theory and Pitfalls in the Specification of Technologies." *Journal of Econometrics*, Vol. 3 (1975), pp. 105-121.
- CLARK, C.W. AND MUNRO, G.R. "Fisheries and the Processing Sector: Some Implications for Management Policy." *Bell Journal of Economics*, Vol. 11 (1980), pp. 603-616.
- DENNY, M. AND FUSS, M. "The Use of Approximation Analysis to Test for Separability and the Existence of Consistent Aggregates." *American Economic Review*, Vol. 67 (1977), pp. 404-418.
- AND PINTO, C. "An Aggregate Model with Multiproduct Technologies" in M. Fuss and D. McFadden, eds., *Production Economics: A Dual Approach to Theory and Applications*, Vol. 2, Amsterdam: North-Holland, 1978.
- DEVANY, A., GRAMM, W., SAYING, T., AND SMITHSON, C. "The Impact of Input Regulation: The Case of the U.S. Dental Industry." *Journal of Law and Economics*, Vol. 20 (1982), pp. 367-381.
- FUSS, M. "The Demand for Energy in Canadian Manufacturing: An Example of the Estimation of Production Structures with Many Inputs." *Journal of Econometrics*, Vol. 5 (1977), pp. 89-116.
- KIRKLEY, J. "The Relationship between Management and the Technology in a Multispecies Fishery: The New England, Georges Bank, Multispecies Fishery." Ph.D. Dissertation, University of Maryland, 1986.

- KULATILAKA, N. "Are Observed Technologies at Long-Run Equilibrium? Tests on the Validity of the Static Equilibrium Model." *Journal of Econometrics*, Vol. 25 (1985), pp. 253-268.
- LEE, L. AND PITT, M. "Microeconomic Demand Systems with Binding Nonnegativity Constraints: The Dual Approach." *Econometrica*, Vol. 54 (1986), pp. 1237-1242.
- LOPEZ, R.E. "Estimating Substitution and Expansion Effects Using a Profit Function Framework." *American Journal of Agricultural Economics*, Vol. 66 (1984), pp. 358-367.
- . "Structural Implications of a Class of Flexible Functional Forms for Profit Functions." *International Economic Review*, Vol. 26 (1985), pp. 593-601.
- MCFADDEN, D. "Cost, Revenue, and Profit Functions" in M. Fuss and D. McFadden, eds., *Production Economics: A Dual Approach to Theory and Applications*, Vol. 1, Amsterdam: North-Holland, 1978.
- MOSS, P. AND TERKLA, D. "Income and Employment Change in the New England Fishing Industry." *Ocean Development and International Law*, Vol. 15 (1985), pp. 37-59.
- SAKAI, Y. "Substitution and Expansion Effects in Production Theory: The Case of Joint Production." *Journal of Economic Theory*, Vol. 9 (1974), pp. 255-274.
- SQUIRES, D. "Long-Run Profit Functions for Multiproduct Firms." *American Journal of Agricultural Economics*, forthcoming.
- WALES, T.J. "On the Flexibility of Flexible Functional Forms: An Empirical Approach." *Journal of Econometrics*, Vol. 5 (1977), pp. 183-193.
- WEAVER, R.E. "Multiple Input, Multiple Output Production Choices, and Technology in the U.S. Wheat Region." *American Journal of Agricultural Economics*, Vol. 65 (1983), pp. 45-56.
- WEITZMAN, M. "Prices vs. Quantities." *Review of Economic Studies*, Vol. 41 (1974), pp. 50-65.
- WILSON, J.A. "Adaptation to Uncertainty and Small Numbers Exchange: The New England Fresh Fish Market." *Bell Journal of Economics*, Vol. 11 (1980), pp. 491-504.

MODELING THE SUSTAINABLE HARVEST OF FEMALE POLAR BEARS

MITCHELL K. TAYLOR, Northwest Territories Department of Renewable Resources, Wildlife Management Division, Yellowknife, Northwest Territories X1A 2L9, Canada

DOUGLAS P. DeMASTER, U.S. Marine Mammal Commission, 1625 1 Street N.W., Washington, D.C. 20006

FRED L. BUNNELL, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia V6T 1W5, Canada

RAYMOND E. SCHWEINSBURG, R.R. #1, Site 20, Comp. 9, Whitehorse, Yukon Y1A 4Z6, Canada

Abstract: We explored the boundaries of sustainable harvest of polar bears (*Ursus maritimus*) by considering a range of values for population parameters in a discrete, age specific model structured to mimic polar bear life history. Survival rate of adult females is the predominant factor affecting population growth rate and sustainable harvest of polar bears although other factors may also be significant; e.g., cub survival, litter size, and age of 1st reproduction. The parameter of least importance is litter production rate. Deferred reproduction has a small effect on population growth rate. These findings are consistent with theoretical predictions for populations experiencing density independent mortality mainly restricted to juveniles. The critical issue, when considering the long-term effect of any harvest, is the effect on numbers of breeding females. Under optimal conditions the sustainable yield of adult female polar bears is typically < 1.6% of the total population.

J. WILDL. MANAGE. 51(4):811-820

We use a model to explore the constraints that polar bear life history structure places on sustainable rates of harvest. We develop a mathematical description of polar bear life history, including harvest as a separate source of mortality. By simulating several harvest types, the model yields information on the effects of harvest types and on the sensitivity of the harvest to changes in vital rates (parameter values). Additionally, a "best case" scenario can be devel-

oped using maximum values for survival and reproduction.

Funding for this work was provided by the Norsk Polarinstitutt, Dep. Renewable Resour., Gov. Northwest Territ., the Univ. British Columbia, and the Mich. State Agric. Exp. Stn. We thank S. C. Amstrup, M. C. S. Kingsley, T. Larsen, L. J. Lee, J. W. Lentfer, P. E. Mills, N. A. Oritsland, M. A. Ramsay, I. G. Stirling, and K. Ugland for their comments and for discussions

that led to this work. M. Bromley, N. J. Lunn, and J. S. Pin edited the text. C. L. Locke and J. E. Troje prepared the figures.

The life history pattern of polar bears is typical of species in which environmental fluctuations strongly affect recruitment rate and survival of the young (Hairston et al. 1970; Schaffer 1974a,b; Stearns 1977; Horn 1978; Goodman 1979, 1981). Polar bears are a long-lived, late maturing species with a low rate of annual recruitment (DeMaster and Stirling 1981).

Polar bears exhibit "birth pulse" (Caughley 1977) reproduction. Typically, a small fraction of polar bear females breed for the 1st time at age 3, and slightly more begin breeding at age 4. Generally all females breed at adult rates from age 5 onwards (initial age = 0). However, age specific litter production rates vary according to environmental conditions (Stirling et al. 1975, 1977, 1978).

During the 1st 2 years following birth, cubs remain with the female and she is unavailable for breeding. Some females with cubs lose their litters and become available for breeding at the next season. Females with 2-year-old cubs are ready for breeding because virtually all cubs are weaned at 2.5 years (Stirling et al. 1975, DeMaster and Stirling 1981). In any given year, however, 30–60% of the available adult females do not breed or are not impregnated (Lentfer et al. 1980; I. Stirling, pers. commun.)

The breeding season for polar bears is from early spring to early summer. Cubs are born in late December or January (Lønø 1970, Lentfer 1976) and are called cubs-of-the-year or COY's to distinguish them from older cubs. Data from captive polar bears suggest that, typically, 2 young are born (Kostyan 1954). However, because of intrauterine and den mortality, the average litter size of adult females ranges from 1.58 to 1.87 (Lønø 1970; Stirling et al. 1975, 1977, pers. commun.; Lentfer 1976; Lentfer et al. 1980). The sex ratio of cubs is 1:1 (DeMaster and Stirling 1981). The long period of female parental care results in high 1st year survival rates of cubs (0.70–0.85) (DeMaster and Stirling 1983). Annual survival rate estimates range from 0.76 to 0.95 for subadults and adults (Stirling et al. 1975, DeMaster et al. 1980, Lentfer et al. 1980).

DESCRIPTION OF MODEL

The use of reproduction terminology is not consistent in the literature. Fecundity, natality,

birth, reproduction, and recruitment rates are all used to refer to the female offspring in the initial age class at the time of census. The traditional census period for polar bears occurs just after adult females emerge from their dens in spring. In the context of life-table projections, we feel that recruitment rate is the most appropriate and descriptive term.

Our definition of age specific recruitment rate m_x is:

$$m_x = \frac{N_{x-1,t-1} \cdot A_{x-1} \cdot B_{x-1} \cdot p_{x-1} \cdot L_x}{N_{x,t}} \\ = A_{x-1} \cdot B_{x-1} \cdot L_x.$$

The number of COY's at time t , produced by x -year-old females is then:

$$= m_x \cdot N_{x,t},$$

and the total number of COY's produced is:

$$= \sum_{x=1}^w m_x \cdot N_{x,t},$$

where

- 0 = initial age class,
- w = final age class = 23,
- x = discrete age class,
- t = discrete time interval (i.e., 1 year),
- $N_{x,t}$ = number of females of age x at time t ,
- p_{x-1} = fraction of $N_{x-1,t-1}$ that survive to be $N_{x,t}$ (i.e., annual survival rate),
- m_x = age specific recruitment rate of $N_{x,t}$ (i.e., the no. of $N_{0,t}/N_{x,t}$ at the time of census),
- A_{x-1} = proportion of $N_{x-1,t-1}$ available for breeding,
- B_{x-1} = proportion of $A_{x-1,t-1}$ available for reproduction at time $t-1$ that would produce recruits at time t if all $N_{x-1,t-1}$ survived to be $N_{x,t}$ (i.e., litter production rates), and
- L_x = litter size of female recruits produced by those $N_{x,t}$ that produce recruits.

Taylor et al. (1987a) document systematic errors that can occur when multi-year reproduction cycles are summarized with mean annual rates. To avoid this type of error our parameters were chosen to mimic, not summarize, the reproduction cycle of arctic polar bears. Our age specific recruitment rate comprises 3 components: availability to reproduce (A), litter production rate of reproducing females (B), and litter size of recruits (L) at time of census.

Table 1. Sustainable harvest (as % of the total pop) for a nonselective harvest of adult female polar bears for a range of adult survival rates and other parameters. (These pop parameter values are representative of high arctic pops not experiencing density effects during favorable environmental conditions. The projected sustainable harvests may be interpreted as maximal rates.)

Parameter set	Ad F survival rate									
	0.90	0.91	0.92	0.93	0.94	0.95	0.96	0.97	0.98	0.99
A ^a	0.0	0.0	0.0	0.20	0.58	0.91	1.23	1.50	1.75	1.94
B ^b	0.0	0.26	0.65	0.99	1.30	1.59	1.83	2.05	2.22	2.36
										2.48

^a Individual cub-of-year (COY) survival rate = 0.85, individual yrl survival rate = 0.85, COY whole litter survival rate = 0.90, yrl whole litter survival rate = 0.90, adult litter production rate = 0.70, age 3 litter production rate = 0.15, age 4 litter production rate = 0.30, litter size of COY's = 1.80, and age of adult reproduction = 5+

^b Individual cub-of-year (COY) survival rate = 0.95, individual yrl survival rate = 0.95, COY whole litter survival rate = 0.90, yrl whole litter survival rate = 0.95, adult litter production rate = 0.70, age 3 litter production rate = 0.15, age 4 litter production rate = 0.30, litter size of COY's = 1.80, and age of adult reproduction = 5+

Survival Rates

Cub survival rates, adult female survival rates, litter size, and litter production rates determine the fraction of females available for breeding, and thereby recruitment. As cub and litter survival rates increase, the average breeding interval increases and the number of females available for breeding in any year decreases.

Failure to become inseminated, failure to be fertilized, resorption of the fetus, intrauterine mortality, and cub mortality inside the den all reduce the estimate of litter production rate. For each age class the fraction of breeding, nursing, and surviving females was monitored. The harvest was subtracted from the appropriate sex and age strata of the population vectors.

Cub survival rate was divided into 3 types:

1. survival rate of mother (death of F results in loss of COY or yrl litters),
2. loss of whole litters as units given that the mother survived (litter survival rate or p_{litter}), and
3. survival rate of individual cubs given that the mother survived and the litter was not lost as a unit ($p_{\text{individual}}$).

Abandonment of single cub litters (Tait 1980) has not been observed in polar bears and was not included in the model.

Adult survival was assumed to be constant from age 2 to 23. Cub survival rate and litter survival rate were age specific for both COY's and yearlings. Litter production rate and litter size were constant from sexual maturity to age 23. The sex ratio of cubs was 1:1 in all cases.

Model Parameterization

The sustainable harvest can be determined for any configuration of parameters that gives a population growth rate >1.0 . We selected a set of representative parameter values (Taylor

et al. 1987b), then explored the sensitivity of sustainable harvest to variation in each parameter. The effect of variation of a particular parameter depends on the values of the other vital parameters. Our results are particular to the parameter values specified as representative. However, our results are conservative because most vital rates chosen as representative were near their maximum observed values. Substantial reduction of the life history parameter values used in this paper would result in a declining population, even with no harvest.

The population parameters shown in Table 1 were used as representative of polar bear populations not experiencing density effects in favorable environments (Stirling et al. 1978, Lentfer et al. 1980, Taylor 1982, DeMaster and Stirling 1983, Taylor et al. 1987b). The reproductive parameter values and the model structure are inappropriate for Hudson Bay polar bears, which typically wean cubs as yearlings and have 3-cub litters approximately 10% of the time (Ramsay and Stirling 1983).

Projections of a Sustainable Harvest

There can be no sustainable harvest if population growth rate is ≤ 1.0 . The relationship between population size (N), population growth (λ), annual recruitment $\{(\lambda - 1) \cdot N\}$, and sustainable yield (Y) is:

$$Y = \{(\lambda - 1) \cdot N\} \cdot X,$$

where X is a variable adjusting for the sex, age, and social composition of the harvest. Leslie (1945) showed that if all sex and age classes are taken in the same frequency as they exist in the population, X would equal unity. Sex and social strata, identified for each age class, were categorized as males, females without cubs, females with COY's, females with yearlings, and females with 2-year-olds. A category of bears without

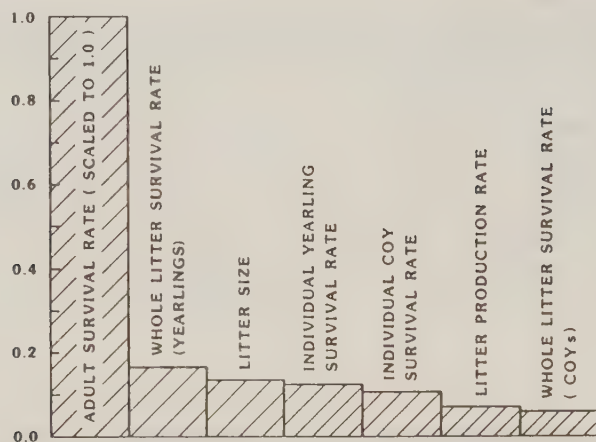


Fig. 1. The mean effects of unit change in polar bear population parameters on sustainable harvest rate are shown relative to adult survival rate (i.e., $\bar{x}$ effect from unit change in ad survival rate scaled to 1.0). Calculation procedures are given in the text and the numerical values for the bars shown are given in Table 1.

cubs (i.e., M and F) was also identified. Harvested animals of each category were taken according to the abundance of each adult (3+ years) age class. If harvested females were accompanied by COY's or yearlings, those cubs were also counted as harvested, since they could not survive on their own. Harvested animals were subtracted from the population vector. The categories of harvest were: (1) bears without cubs (includes M and F without cubs); (2) females with COY's; (3) females with yearlings; (4) females with 2-year olds; and (5) females without cubs.

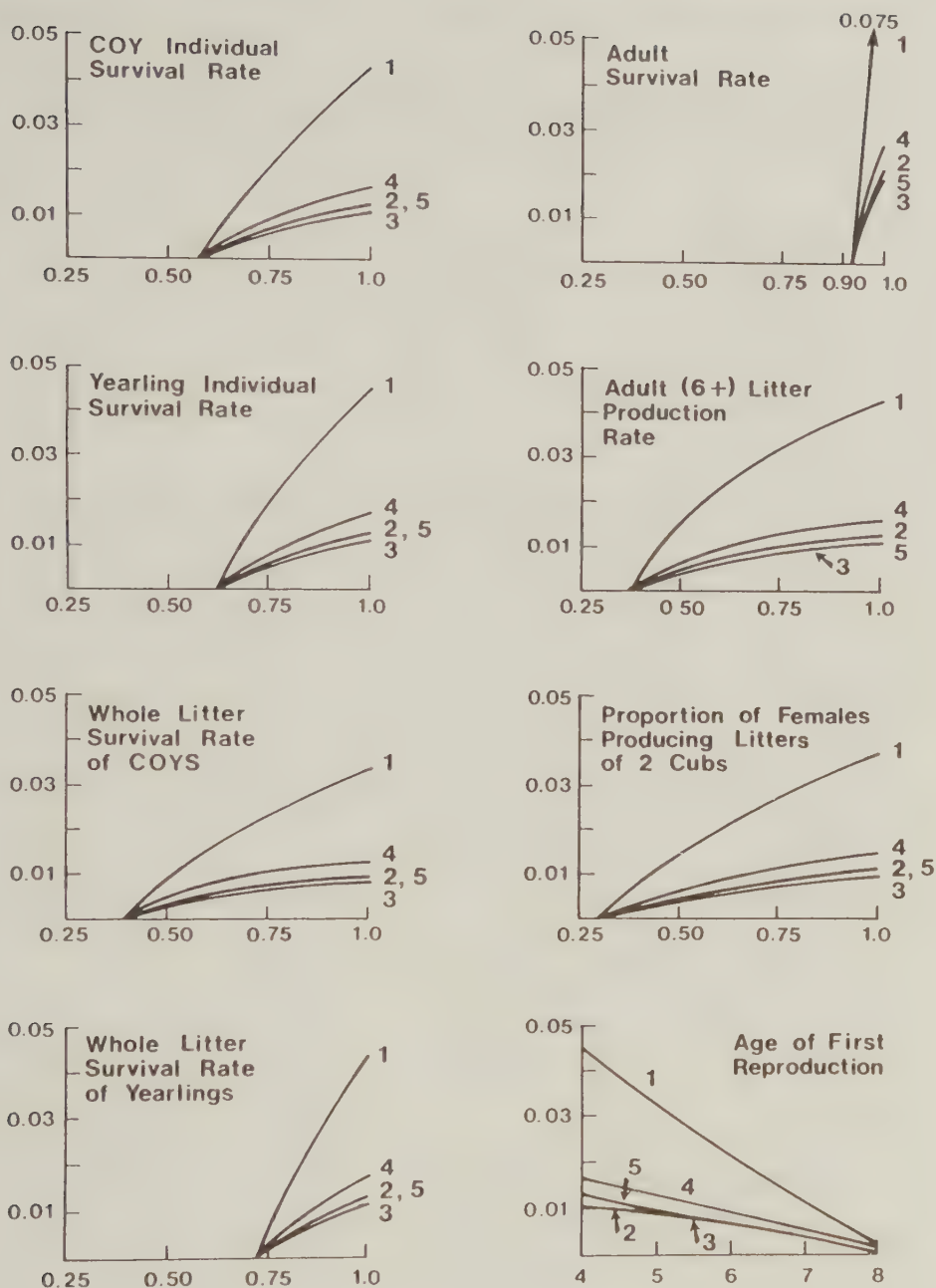
Sustainable yield was expressed as percent of total population taken as adult (age 3+) females of the type specified. Starting conditions for the simulations were determined by the stable age distribution specified by the parameter values. A convergence algorithm was employed to find the sustainable harvest of a particular type. Only the parameter being examined was varied from the default values during a simulation. The range of responses gave the sensitivity of each harvest type to the population parameters. In addition, the relative impact of each harvest type was observed.

The effect of a unit change in each parameter on sustainable harvest was indexed as the absolute value of the slope of the line between the maximum harvest point (parameter value = 1.0) and the minimum harvest point (pop growth rate = 1.0). The slopes recorded for each parameter were scaled by dividing each by the

maximum slope recorded for any parameter, e.g., ad survival rate. The scaled index was thus relative to the adult survival rate slope, defined as 1.0. The index neglected nonlinearity in the sensitivity curve and could not treat age of 1st reproduction (range = 4–8) in a manner consistent with the other parameters, which ranged between 0.0 and 1.0. Because litters have either 1 or 2 cubs, litter size could be represented as the probability of 2-COY rather than 1-COY litters.

RESULTS

Sustainable harvest was most affected by changes in adult female survival rate (Fig. 1). Litter survival rate of yearlings, litter size, individual yearling survival rate, and individual COY survival rate were between 10 and 16.5% as influential as adult survival rate (Fig. 1). Changes in litter production rate and whole litter survival rate of COY's had only 6–7% the effect of changes in the adult survival rate (Fig. 1). Age of 1st reproduction was comparable in percent effect on sustainable harvest to litter survival rate of yearlings, individual survival rate of yearlings, individual COY survival rate, and litter size (Fig. 1). Harvest type had a minimal effect on the sensitivity of harvest rate to population parameters (Table 2). The sensitivity curves (vs. parameter values) were nonlinear for each harvest type (Fig. 2). The relative effects of harvest types converged at the point where



Parameter Value

Fig. 2. Sustainable harvest (as % of the total pop) for 5 harvest types are given as functions of 8 polar bear population parameters. The 5 types of harvest were: (1) bears without cubs (M + F without cubs), (2) female with COY's, (3) female with yearlings, (4) female with 2-year olds, and (5) female without cubs. The parameters and their values were Parameter Set A in Table 1. (These pop parameter values are representative of arctic pops not experiencing density effects during favorable environmental conditions. The projected sustainable harvests may be interpreted as max. rates.)

Table 2. The relative effects of polar bear population parameters (ad survival rate effects scaled to 1.0) are given for 5 harvest types. Calculation procedures for the relative effect of population parameters are given in the text. Column 6 contains the mean and column 7 the standard error of the parameter effect given by pooling all 5 harvest types.

Parameter	Harvest type ^a					<i>s</i>	Pooled SE
	1	2	3	4	5		
Ad F survival rate	1.00	1.00	1.00	1.00	1.00	1.00	0.00
Whole litter survival (yrl)	0.1539	0.1620	0.1598	0.1761	0.1753	0.1654	0.0098
COY litter size	0.1232	0.1319	0.1268	0.1423	0.1421	0.1332	0.0087
Yrl survival rate	0.1176	0.1206	0.1162	0.1305	0.1327	0.1235	0.0076
COY survival rate	0.0996	0.1033	0.0997	0.1096	0.1116	0.1048	0.0056
Litter production rate	0.0666	0.0707	0.0679	0.0724	0.0701	0.0695	0.0023
Whole litter survival (COY's)	0.0555	0.0573	0.0558	0.0610	0.0611	0.0581	0.0027

^a 1 = bears without cubs (M and F without cubs), 2 = F with cubs-of-the-year (COY), 3 = F with yr1, 4 = F with 2-year-olds, and 5 = F with no cubs.

population growth rate (λ) equalled 1.0 and no harvest of females could be sustained.

The absolute differences in sustainable harvest among the various female family group strata were small (Table 2). Harvests of females with 2-year olds could be higher because we assumed the cubs were not killed and could live on their own. Harvesting females with COY's and females with no cubs was nearly equivalent. Females with yearlings were able to sustain the lowest rate of harvest. The bears without cubs category sustained high levels of harvest because most of the animals taken were males. Although the effects of harvest type were particular to each combination of population parameters, the effect of the harvest type appeared robust (Table 2, Fig. 2).

Sustainable levels of a nonselective harvest of adult females were determined for a range of adult survival rates using the default values for the other population parameters (Fig. 3). The nonselective harvest was similar in effect to the harvest of females with COY's (Type 2) and females with no cubs (Type 5).

The mean reproduction interval (Taylor 1987b) (years between litters produced) and mean breeding interval (Taylor 1987b) (years between availability for mating) were calculated for a range of survival values using the default parameters (Fig. 4). The reciprocal of mean reproduction interval is sometimes used as a nonweighted estimate (for age) of reproduction rate (Caughley 1977). A nonweighted estimate of annual recruitment rate can be calculated by multiplying the reproduction rate times the mean number of females/litter. Similarly, a nonweighted breeding rate may be calculated.

Estimates of mean annual recruitment rates ranged from 0.226 (Lentfer et al. 1980) to 0.274

(DeMaster and Stirling 1981). Estimates of reproduction interval have varied from 3.5 to 3.8 years (Lentfer 1976, Lentfer et al. 1980). DeMaster and Stirling (1981) give an estimate of reproduction interval of 3.1 years; however, in our terminology this is called breeding rather than reproduction interval (Taylor et al. 1987b). The minimum possible reproduction interval for arctic polar bears is 3.0 and the maximum possible recruitment rate is 0.333 (DeMaster and Stirling 1981). The range of reproduction intervals calculated, using the default parameter estimates, ranged from 3.47 (ad survival = 1.0) to 3.32 (ad survival = 0.81). Unweighted annual recruitment rates ranged between 0.288 (ad survival = 1.0) and 0.301 (ad survival = 0.81).

DISCUSSION

The life history strategy of polar bears is consistent with that predicted for animals that experience fluctuations in recruitment due to an unpredictable environment (Stearns 1977). The arctic environment undergoes large-scale fluctuations between and within years (Vibe 1967). Polar bears are well adapted to and are in delicate ecological balance with their environment. This balance was particularly apparent during years of locally abundant ice, such as 1974 and 1975 (Stirling et al. 1975, 1977; Uspenskii 1977; Smith 1980) and years of locally sparse ice, such as 1979 (S. M. Uspenskii, pers. commun.). During those years, litter production rate and sub-adult (age 3–5) survival rates were reduced. For species exploiting a niche requiring a large body and behavioral plasticity, the evolutionary response to an unpredictable environment can include delayed maturity, reduced reproductive effort, and fewer young (Stearns 1977). Polar

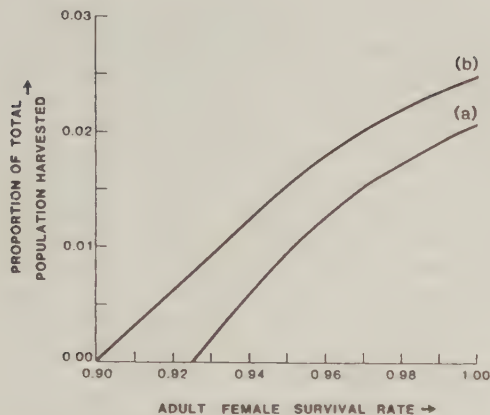


Fig. 3 "Sustainable harvest" refers to the percent of the total polar bear population (young and males included) that is harvested as adult females. "Harvested" also includes problem bears and illegally taken bears. In this example adult females were harvested without regard to maternal status; i.e., the harvest was nonselective. The percent of sustainable adult (age 3+) female harvest is given for 2 population parameter sets, A and B, set to maximum observed for all populations studied where females are taken according to abundance; i.e., no family status selectivity.

bear life history strategy is typified by high adult survival rates and minimal effects on mean population growth rate due to fluctuations in recruitment.

Polar bear recruitment depends on the age specific past history of each female age class. Environmental instability affects the number of females available for breeding, and the number that actually produce offspring, by affecting survival rates of cubs and the nutritional status of breeding females (Stirling et al. 1975, Lentfer et al. 1980, Larsen 1985). Sustainable harvest is sensitive to litter size, but relatively insensitive to the proportion of females, available for breeding in a given year, that breed successfully. This result is important because: (1) it identifies deferred reproduction as the least costly method of avoiding the nutritional drain of maternity and the subsequent 2.5 years of rearing cubs; and (2) it raises the question of why female polar bears in most populations have only 2 cubs. Although almost 10% of the subarctic Cape Churchill population have 3-cub litters (Ramsay and Stirling 1983), 3-cub litters are rare in the high arctic areas of Siberia, Greenland, Svalbard, Alaska, and Canada.

Polar bears evolved from brown bears (*Ursus arctos*) (Kurten 1964), which often have 3 or more cubs/litter, but Bunnell and Tait (1981)

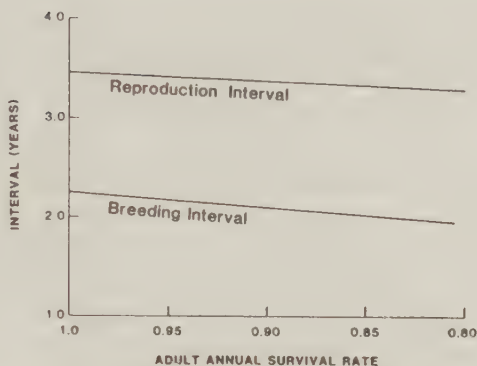


Fig. 4. The mean interval between reproduction (producing a litter) and breeding (being available to breed) is a function of adult survival, cub survival (litter loss rates), and litter production rate (fraction of those available that actually produce a litter). The reproduction and breeding intervals produced by the default parameter values (Set A in Table 1) are given for a range of survival rates.

suggested that nutritional stress in winter was responsible for the 2-cub maximum litter size in arctic areas. In Hudson Bay polar bears are forced on shore near Cape Churchill from ice-out in mid-summer until ice-up in mid-November. Ramsay and Stirling (1983) speculated that seals might be exceptionally abundant or available in this area to allow rearing 3-cub litters and weaning cubs as yearlings. Estimates of the trade-offs between adult survival rate and breeding success have not been made. If we accept that such energetic trade-offs do exist (Bunnell and Tait 1981), then we can understand the relatively long period of maturation as a similar trade-off. Immediate reproductive output with low probability of success is exchanged for increased likelihood of survival. Bunnell and Tait (1981) note a strong correlation between litter size and weight in brown and black (*Ursus americanus*) bears.

The effects of environmental stress on survival rates apparently occur most strongly in subadults having no mother to intercede, no breeding success to "barter," and a smaller store of fat reserves (Stirling et al. 1975, Uspenskii 1977, Smith 1980). Observations of density dependent and density independent effects on populations of other marine mammals indicate that these effects are typically 1st manifest as reductions in annual breeding success and reduced subadult survival rates (Eberhardt 1977, Eberhardt and Siniff 1977). Reduced survival rates of subadult polar bears have a greater impact on pop-

ulation growth rate and sustainable harvest than reduced litter production rates. Subadult survival rates may be important in density independent fluctuations of polar bear populations.

Our model did not discriminate between subadult (ages 3–4) and adult survival rates. Although subadult age classes are relatively abundant, they do not produce many recruits. Reduction of subadult survival rates is roughly equivalent to a fractional reduction in adult survival rates. The fraction would be the ratio of subadults:adults. Subadults are more vulnerable than adults to environmental effects and are the age strata that most often become "problem bears" (Stenhouse 1983). As problem bears, they have reduced expectations of survival. Problem bear mortality may be of increasing significance as northern development proceeds.

The mechanism of density dependent regulation of polar bear populations is an open question. Any mathematical functions chosen to describe it are, at best, conjecture and, at worst, misleading. The allure of using compensatory models in harvest analysis is that a *maximum* sustainable yield can be calculated. Density dependent models can be inappropriate for populations in environments perceived as unpredictable, because such populations rarely are numerous enough to experience density effects (Andrewartha and Birch 1954, Wilbur et al. 1974). Additionally, Eberhardt and Siniff (1977) and Fowler (1981a,b) marshal both arguments, and evidence suggesting that the effect of increased number is minimal at low and intermediate densities for long-lived animals with delayed reproduction. The vital parameter values specified in model (Table 1) are representative of a population not experiencing density effects in a favorable environment. Thus, sustainable harvest projections represent a best case situation. Vital parameter rates were chosen as the maximum values from published (DeMaster and Stirling 1981, Taylor et al. 1987b) and unpublished analyses (I. Stirling, pers. commun.). The mean annual recruitment rates stemming from our default values (0.288–0.301) exceed those reported in the literature (0.226–0.274) (Lentfer et al. 1980, DeMaster and Stirling 1981). Assuming that adult survival rate equals 0.95, the stable-age, unharvested, population growth rate was 1.017 for Parameter Set A (Table 1) and 1.051 for Parameter Set B (Table 1).

There is some suggestion of sampling bias

against family groups (I. Stirling, pers. commun.). This bias would cause litter production rates, and subsequently recruitment rates, to be underestimated. We elected to use published values because the existence or extent of this bias has not been quantified. It could be argued that our assumed rates of COY and yearling survival and litter production are not absolute maxima. However, because of the relative insensitivity of harvest rates to changes in either of these parameters (Figs. 1 and 2), we feel that our conclusions are reasonably robust.

Mating in polar bears is promiscuous, thus recruitment is primarily a function of the number of adult females. A male-only harvest would not affect annual recruitment until males were in short supply. However, some hunters may not distinguish males from females without cubs and other hunters take females on opportunity. Pregnant females are particularly vulnerable to shore-based hunters when they return to land for maternity denning. Adult females are especially important to population growth rate because reproductive maturity indicates survival through the vulnerable subadult period. Females have few litters because of sustained parental care given to their cubs and the possibility of deferring reproduction during bad years or between litters. Loss of a female with cubs is only slightly worse, in terms of loss of recruitment to the population, than loss of a female unencumbered with cubs (Table 2).

The breeding population is augmented by approximately 25% of the annual recruitment rate because only 50% of the cubs produced are female, and 4–6 years of annual mortality occur before the juvenile and vulnerable subadult classes reach maturity (Taylor 1982). If adult females were immortal, the breeding segment of the population would receive an annual increment of only 2.5% of the total population. Assuming a more realistic (i.e., 5.0%) natural mortality, the annual increment of adult females would be between 1.0 and 1.6% of the total population. This annual increment is the sustainable harvest of adult females.

Although the effect of population parameters on growth rate depends on the values of the other parameters, the ranking (Table 1) appears robust through the range of biologically plausible values. The dependence of polar bear life history strategy on constantly high adult survival rates causes polar bears to be particularly

vulnerable to overharvest. The nature or existence of compensatory mechanisms is not known for any polar bear population. Conservative management and comparisons with other long-lived species suggest that noncompensatory harvest models are most appropriate for polar bears.

The structure of polar bear life history biology reduces the question of sustainable harvest to essentially 3 factors: (1) population numbers; (2) adult female survival rates; and (3) number of harvested bears that are adult females. As Figure 2 and Table 2 indicate, the family status of a harvested female is relatively unimportant to the sustainable harvest level. Within the range of biologically reasonable survival and recruitment values, polar bear populations sustain <1.6% harvest of adult (3+ years) females. This value can only be increased by about 1% by assuming that adult females are immortal except for harvest.

The implications for existing harvests have already been addressed for 1 polar bear population in North America. The Inuit communities of Clyde River and Broughton Island, on northeast Baffin Island, have voluntarily reduced their harvest of polar bears to a sustainable level. Similar measures may also be required in other areas to avoid population depletion.

LITERATURE CITED

- ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. The distribution and abundance of animals. Univ. Chicago Press, Chicago, Ill. 782pp.
- BUNNELL, F. L., AND D. E. N. TAIT. 1981. Population dynamics of bears—implications. Pages 75–98 in C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley & Sons, Inc., New York, N.Y.
- CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, Inc., New York, N.Y. 234pp.
- DEMASTER, D. P., M. C. S. KINGSLEY, AND I. STIRLING. 1980. A multiple mark and recapture estimate applied to polar bears. Can. J. Zool. 58: 633–638.
- , AND I. STIRLING. 1981. *Ursus maritimus*. Mammal. Species, Am. Soc. Mammal. 145:1–8.
- , AND ———. 1983. The estimation of survival and litter size of polar bear cubs. Int. Conf. Bear Res. and Manage. 5:260–263.
- ENERHARDT, L. L. 1977. Optimal policy for conservation of large mammals with special reference to marine ecosystems. Environ. Conserv. 4: 205–212.
- , AND D. B. SINIFF. 1977. Population dynamics and marine mammal management policies. J. Fish. Res. Board Can. 34:183–190.
- FOWLER, C. W. 1981a. Comparative population dynamics in large mammals. Pages 437–455 in C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley & Sons, Inc., New York, N.Y.
- . 1981b. Density dependence as related to life history strategy. Ecology 62:602–610.
- GOODMAN, D. 1979. Regulating reproductive effort in a changing environment. Am. Nat. 113:735–748.
- . 1981. Life history analysis of large mammals. Pages 414–436 in C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley & Sons, Inc., New York, N.Y.
- HAIRSTON, N. G., D. W. TINKLE, AND H. M. WILBUR. 1970. Natural selection and the parameters of population growth. J. Wildl. Manage. 34:681–690.
- HORN, H. S. 1978. Optimal tactics of reproduction and life-history. Pages 411–429 in J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. Blackwell Sci. Publ., Oxford, U.K.
- KOSTYAN, E. 1954. New data on the reproduction of the polar bear. Zoologische Zhurnal 33:207.
- KURTEN, B. 1964. The evolution of the polar bear, *U. maritimus* Phipps. Acta Zool. Fennica 108:3–30.
- LARSEN, T. 1985. Abundance, range and population biology of the polar bear (*Ursus maritimus*) in the Svalbard area. Ph.D. Thesis, Norsk Polarinstitutt, Oslo, Norway. 247pp.
- LENTFER, J. W. 1976. Polar bear reproductive biology and denning. Alaska Dep. Fish and Game, Final Rep. 5.4R. 22pp.
- , R. J. HENSEL, J. R. GILBERT, AND F. E. SORENSON. 1980. Population characteristics of Alaskan polar bears. Int. Conf. Bear Res. and Manage. 4:109–117.
- LESLIE, P. H. 1945. On the use of matrices in certain population mathematics. Biometrika 33:183–212.
- LØNØ, O. 1970. The polar bear in the Svalbard area. Norsk Polarinstitutt Skrift 149:1–103.
- RAMSAY, M. A., AND I. STIRLING. 1983. Reproduction biology and ecology of female polar bears in western Hudson Bay. The Can. Nat. 109:941–946.
- SCHAEFFER, W. M. 1974a. Optimal reproductive effort in fluctuating environments. Am. Nat. 108: 783–790.
- . 1974b. Selection for optimal life histories: the effects of age structure. Ecology 55:291–303.
- SMITH, T. G. 1980. Polar bear predation of ringed and bearded seals in the land-fast sea ice habitat. Can. J. Zool. 58:2201–2209.
- STEARNS, S. C. 1977. The evolution of life-history traits. Annu. Rev. Ecol. and Syst. 8:145–171.
- STENHOUSE, G. 1983. The N.W.T. bear deterrent and detection research program. NWT Wildl. Notes 8:1–3.
- STIRLING, I., D. ANDRIASHEK, P. LATOUR, AND W. CALVERT. 1975. Distribution and abundance of polar bears in the eastern Beaufort. Beaufort Sea Tech. Rep. 2:1–59.
- , W. R. ARCHIBALD, AND D. DEMASTER. 1977.

- Distribution and abundance of seals in the eastern Beaufort Sea. Can. J. Zool. 34:976-988.
- , R. E. SCHWEINSBURG, W. CALVERT, AND H. P. L. KILJAAN. 1978. Population ecology of the polar bear along the proposed Arctic Island Gas Pipeline Route. Final Rep. to Environ. Manage. Serv., Dep. Environ., Edmonton, Alb. 93pp.
- TAIT, D. E. N. 1980. Abandonment as a reproductive tactic—the example of grizzly bears. Am. Nat. 115:800-808.
- TAYLOR M. K. 1982. The distribution and abundance of polar bears (*Ursus maritimus*) in the Beaufort and Chukchi Seas. Ph.D Thesis, Univ. Minnesota, Minneapolis. 353pp.
- , J. S. CARLEY, AND F. L. BUNNELL. 1987a. Correct and incorrect use of recruitment rates for marine mammals. Mar. Mammal Sci. 3(2): 171-178.
- , F. L. BUNNELL, D. P. DEMASTER, AND J. SMITH. 1987b. ANURSUS: a population and analysis system for polar bears (*Ursus maritimus*). Int. Conf. Bear Res. and Manage. 7:In Press.
- USPENSKII, S. M. 1977. The polar bear. Nauka, Moscow. 107pp. [Eng. trans. by Can. Wildl. Serv., 1978.]
- VIBE, C. 1967. Arctic animals in relation to climatic fluctuations. Meddeleser om Gronland. 227pp.
- WILBUR, H. M., D. W. TINKLE AND J. P. COLLINS. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. Am. Nat. 108:805-817.

Received 6 December 1985.

Accepted 3 March 1987.

FEEDING ECOLOGY AND GROWTH ENERGETICS OF LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

GAIL H. THEILACKER¹

ABSTRACT

The relation between prey consumption and gross growth efficiency was determined for first-feeding northern anchovy, *Engraulis mordax*, fed rotifers for 2 weeks. Larval length- and weight-specific daily consumption, given as prey numbers, dry weight, and caloric value, were less for the 2/mL rotifer diet and gut residence time was longer, resulting in a higher gross growth efficiency (0.46) than the 25/mL rotifer diet (0.37). Daily percent increases in dry weight for northern anchovy fed rotifers were 15% at the low density and 21% at the high density. Northern anchovy grew the most, 23% per day, when fed 2/mL copepods, but their length-specific weight was less than those fed on the rotifer diets. Equations for the rotifer and copepod diets are given for calculating growth in length and weight, size-specific stomach contents related to feeding period, and daily food consumption based on empirically determined gastric evacuation rates. Respiration was measured directly and indirectly, by using a starvation analysis to measure the caloric equivalent of metabolism; results from both methods agreed. A power equation was used to express metabolism as a function of dry weight. Estimates of gross growth efficiencies showed that larval northern anchovy may exhibit a high growth rate or a high efficiency, but not both at the same time. Information also is given on increase in size of prey selected as northern anchovy larvae grow.

Measurements of gross-growth efficiency (calories of growth/calories consumed) of fishes are a good indicator of the adequacy of their diet and state of health (Brett and Groves 1979). Generally a favorable environment for larval fish growth can be inferred by using information on growth efficiencies as related to prey densities. A high-growth efficiency is the result of efficient assimilation of food energy for growth, with relatively little energy lost as feces or used in respiration.

A wealth of information is available on larval northern anchovy, *Engraulis mordax*. Research has been directed toward understanding the factors that affect their survival, yet no information exists on the growth efficiency of larval northern anchovy.

Larval northern anchovy have been cultured in the laboratory, and their growth and survival on wild plankton (Kramer and Zweifel 1970; O'Connell and Raymond 1970) and on cultured foods (Lasker et al. 1970; Theilacker and McMaster 1971; Hunter 1976) have been described and compared with their growth in the field (Methot and Kramer 1979). Incubation times, yolk absorption and the onset of feeding (Lasker 1964; Lasker et al. 1970), feeding success and swimming behavior (Hunter 1972) and

their ability to withstand starvation (Hunter 1976; Theilacker and Dorsey 1980) have been studied. Here I describe how variations in prey density affect consumption, growth, and gross growth efficiencies and compare my results to those on other larval fishes.

MATERIALS AND METHODS

The rationale for my experimental design was to avoid known problems that affect interpretation of results of energetic studies. Mainly I determined gut contents directly, which gives a measure of individual variability, rather than by controlling prey level in the tank and estimating feeding by difference in prey numbers over time. To obtain more precise fresh dry weight values for these small larvae, I grouped them by size class to increase the measured weight. I converted the number of prey eaten to width-specific and species-specific fresh dry weights and caloric values, thus precluding problems inherent with feeding rate estimations that use preserved sample weights and/or average prey weights. Because gastric evacuation depends on feeding rates, I conducted the evacuation experiments with actively feeding larvae. In addition, I compared and validated traditional oxygen uptake measurements with a starvation analysis used to estimate the caloric equivalent of metabolism.

¹Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

Larval Rearing

Northern anchovy eggs were spawned by administering hormone injections to a brood stock held at the Southwest Fisheries Center (Leong 1971). Larvae raised from the eggs were kept in 100 L circular, black polypropylene tanks at constant temperature (15.5°C) and photoperiod (12 h/12 h). In this study, I varied the prey type and density. At the onset of feeding, northern anchovy larvae have small mouths that restrict their feeding to small prey (Hunter 1977). Thus for the initial feeding (day 3) all larvae were fed *Gymnodinium splendens*, a naked dinoflagellate having a width of about 50 μm (Lasker et al. 1970), and 2 days later the larvae were fed larger prey. Because it is impossible to quantify the caloric input from *Gymnodinium* directly (digested cells cannot be counted), the experiments began on day 5 when the larger prey could be removed from the fish stomachs, counted, measured, and subsequently expressed as caloric input.

Experimental Design

I conducted five experiments. In the first experiment, rotifers, *Brachionus plicatilis*, at a density of 35/mL were fed for 20 days, and the number of prey eaten was determined. The size of the rotifers was not measured in this initial experiment, but in subsequent experiments, widths of prey eaten were measured. In the second and third experiments, rotifers were offered at densities of 2 and 25/mL respectively for 14 days. In the fourth experiment, copepods, *Tigriopus californicus*, nauplii and copepodites were fed to larvae at a density of 2/mL (usually 1 nauplius and 1 copepodite/mL) for only 9 days instead of 14 days because of problems with the copepod culture. In the fifth experiment, larvae were fed copepods at 0.2/mL for 12 days without the initial addition of *Gymnodinium*. (Mortalities were high on this low density copepod diet, and data are few; high mortalities are consistent with results reported by O'Connell and Raymond [1970] for northern anchovy raised on a similar diet. The addition of a *Chlorella* bloom to this diet improves survival of northern anchovy [Moffatt 1981].)

To estimate larval growth as the increase in standard length, SL, and dry weight, W , larvae were pipetted individually onto a slide and measured while alive. Larvae were then rinsed in distilled water and, to ensure dependable mean dry weight determinations, grouped by size class onto a clean slide. Larvae <5 mm were grouped by 0.2 mm size class, and those >5 mm were grouped by 0.3 mm size class.

Numbers of larvae per group ranged between 2 and 12; the larger the larval weight, the fewer larvae I grouped together. After drying to a constant weight at 60°C (Lovegrove 1966), larvae were removed from the slides by using a single-edged razor blade and weighed on a Cahn electrobalance to $\pm 2 \mu\text{g}$.

Feeding

To estimate feeding rates and daily consumption, each prey item removed from the larva's gut was counted and its width measured. Width is the dimension that limits a fish larva's selection of prey (Beyer 1980; Hunter 1981). Prey defecated onto the slide were included in the total number eaten. Gut contents in dry weight were determined by summing the width-specific weights of the prey eaten each day. I used the width-specific fresh dry weights and caloric values for *Brachionus* and *Tigriopus* given by Theilacker and Kimball (1984) and reproduced here in Table 1.

Because northern anchovy larvae eat continuously, asymptotic curves ($c = C_{\text{max}} \times (1 - e^{-kt})$) were used to describe food intake, i.e., the relation between observed gut contents c and time t , where C_{max} is the asymptotic gut contents (contents in gut at steady state after filling) and k is the instantaneous rate of gut filling. Using Marquardt's algorithm for fitting nonlinear models, parameters C_{max} and k were estimated for 0.5 mm length classes (Table 2). Fish with empty stomachs were included in this analysis because all fish were used in the growth estimates. Daily mean gut contents $\bar{c}$ were calculated by integrating the area beneath

TABLE 1.—Width-specific dry weight and caloric value of rotifers, *Brachionus plicatilis*, and copepods, *Tigriopus californicus*¹.

Prey	Width class μm	Per individual		
		Dry weight μg (SE)	Volume $\times 10^6 \mu\text{m}$	Caloric value $\times 10^{-3}$ cal
<i>Brachionus plicatilis</i> (4.4 cal/mg)				
Rotifers	74.3-109.7	0.10 (0.01)	0.65	0.44
	109.8-146.7	0.22 (0.04)	1.73	0.97
	146.8-183.8	0.41 (0.06)	2.96	1.80
	183.9-195.0	0.47 (0.08)	3.99	2.07
<i>Tigriopus californicus</i> (4.9 cal/mg)				
Nauplii	74.3-109.7	0.04 (0.01)	0.20	0.20
	109.8-146.7	0.13 (0.01)	0.55	0.64
	146.8-183.8	0.25 (0.01)	1.17	1.23
	183.9-195.0	0.38 (0.00)	1.77	1.86
Copepodites	146.8-183.8	0.63 (0.15)	3.38	3.09
	183.9-221.0	1.20 (0.26)	6.21	5.88

¹From Theilacker and Kimball 1984, table 2.

TABLE 2.—Estimates of the asymptotic gut contents ($C_{\max}$) and instantaneous rate of gut filling (k) for northern anchovy (n) fed several diets¹.

Diet	Prey level per mL	SL (mm)	n	Prey number		Prey weight μg	
				$C_{\max}$	k	$C_{\max}$	k
Rotifers ²	35	4.00	89	6.16	0.33		
		5.00	236	9.90	0.32		
		6.00	131	11.91	1.13		
		7.00	219	15.92	3.73		
		8.00	159	28.33	3.78		
		9.00	171	46.36	2.56		
		10.00	89	52.22	1.72		
Rotifers	25	4.25	58	³ 15.55	0.12	1.80	0.29
		4.75	69	7.79	0.67	2.12	0.67
		5.25	54	12.93	0.62	2.36	0.83
		5.75	35	14.01	0.64	2.92	0.58
		6.50	28	16.97	1.96	3.31	3.76
		8.00	32	27.80	1.84	6.68	1.61
Rotifers	2	4.25	33	7.44	0.35	0.50	0.18
		4.75	19	4.97	1.61	1.35	0.98
		5.25	18	8.86	1.29	2.42	0.73
		8.00	16	9.94	1.30	4.00	0.88
Copepods ⁴	2	4.25	21	1.54	1.27	0.08	0.49
		4.75	63	4.89	0.42	0.52	0.37
		5.25	44	4.45	0.45	0.94	0.57
		5.75	32	3.86	0.41	1.15	1.49
		⁵ 6.25	31	4.94	1.01	1.99	0.88
		8.00	14	7.22	1.30	3.66	0.66

¹Includes zero gut contents; observed gut contents c at time $t = C_{\max} \times (1 - e^{-kt})$.²Prey width not measured.³87% rotifers <150 μm width⁴Fish eating *Gymnodinium* exclusively were removed to estimate $C_{\max}$ and k .⁵Copepod concentration <0.1/mL

the curves and dividing by the 12-h feeding period.

Equations were derived for each diet from the relation of $C_{\max}$ and k with fish size and duration of feeding; these equations allow the calculation of gut contents c at time t for all fish lengths between 4 and 8 mm. The parameters (Table 3) were found using the derivative-free nonlinear regression program (BMDPAR) by Biomedical Computer Programs (BMDP, 1981).

Daily consumption F_w was estimated using a modification of an equation for consumption developed by Stauffer (1973) and discussed by Elliott and Persson (1978) and Jobling (1981), $F_w = rt + C_{12}$, where r is the μg evacuated per hour calculated as mean gut contents $\bar{c}$ divided by the empirically determined rate of gastric evacuation (see Evacuation Rates), t is the duration of feeding, and C_{12} is the dry weight of the food remaining in the stomach at the end of the 12-h feeding period.

Growth

Length data for all feeding treatments were fit to exponential growth curves, $SL = l_0 e^{kt}$ where l_0 is length at hatching, k is the instantaneous growth rate and t is the age. Length-weight data were fit to a power equation where weight $W = a(SL)^b$; parameters for the growth equations are given in Table 4.

TABLE 3.—Parameters for equation¹ relating observed gut contents c in μg dry weight at time t to standard length (SL) of northern anchovy fed three diets.

Diet	Age	<i>n</i>	<i>P</i> ₁	(SD)	<i>P</i> ₂	(SD)	<i>P</i> ₃	(SD)	<i>P</i> ₄	(SD)
Rotifers										
25/mL	5-14	280	-1.90	(0.70)	0.51	(0.18)	0.57	(0.16)	0.29	(0.03)
2/mL	5-14	103	—	—	² 0.69	—	0.33	—	0.326	—
Copepods										
2/mL	5-9	171	2.84	(0.88)	-0.39	(0.12)	³ 1.26	³ (0.75)	1.18	(0.10)

$$^1 c = p_3 e^{p_4 SL} (1 - e^{-(p_1 + p_2 \cdot SL)^{p_3}})$$

²($P_1 + P_2$) fixed at 0.69, the mean k from Table 2; asymptotic standard deviations could not be computed because k was held constant.

³ $\times 10^{-3}$

TABLE 4.—Parameters for northern anchovy growth equations where SL is standard length in mm, W is weight in μg , and t is age in days.

Diet	Age (d)	n	Age length $SL = l_0 e^{kt}$				Length-weight $W = a(SL)^b$			
			l_0	(SD)	k	(SD)	a	(SD)	b	(SD)
Rotifers	25/mL	5-14	280	3.06	0.05	0.06	0.001	253	0.197	0.040
	2/mL	5-14	103	3.14	0.07	0.05	0.002	84	0.379	0.030
Copepods	2/mL	5-9	138	3.06	0.15	0.07	0.010	109	0.297	0.097

Metabolism

I determined metabolic rates for the larvae, which ranged in age from first-feeding (3 days after hatching) to 25 days using the Winkler technique. I chose the Winkler technique where large vessel volumes could be used and there was no need to shake the vessels during the experiment, as required for manometric techniques. Pearcy et al. (1969) found no differences between Winkler and Warburg estimates of oxygen consumption. Oxygen consumption was estimated at 16°C during 18-23 h experimental periods with a 12 h light-dark cycle. The respiration vessels were attached to a large, slowly rotating wheel. Young larvae, 0.02-0.14 mg dry weight were tested in 40 mL vessels in groups of 10-50, while larvae older than 16 days (larger than 0.14 mg) were tested individually in 60-150 mL vessels. All fish tested had empty guts. Data were not used when mortalities occurred during the experiment.

To express metabolism (Q) as a function of dry weight, I used a nonlinear regression to fit a power equation to the data (see parameters for Model 1 in Table 5). The data points were weighted by their sample size ($n = 10-50$). The Model 1 fit was unsatisfactory for the whole size range, presumably because each data point for the young larvae ($n = 72$) was a group mean, and the model was significantly weighted toward the young larvae, causing it to overestimate oxygen consumption for the few large larvae ($n = 17$). Because the experimental technique differed (i.e., respiration was measured for groups of young larvae or individual older larvae), I also fitted two separate curves. These curves (Model 2) gave a good fit to the data (Table 5); the Model 2 equation for younger larvae was used in the present study.

An alternate approach for estimating metabolic requirements is to starve larvae of known size (weight), determine the size-specific weight loss, and convert the weight loss to calories. This approach eliminates the need to restrict larval swimming activity in a respiration vessel. Presumably the weight

loss in caloric units would equal the loss due to metabolic costs, excluding the metabolic cost of attacking prey. Using this approach, I fed control northern anchovy larvae ad libitum on *Gymnodinium* and *Brachionus* and starved the test larvae; both groups were maintained in 100 L rearing tanks at 15.5°C. Live standard length and dry weight of groups of the same length were measured daily, as described earlier in this Methods section, for 10-50 larvae sampled daily from each treatment.

I calculated the caloric equivalent of northern anchovy tissue using the caloric values given by Hunter and Leong (1981) for fat-free anchovy tissue, 4.129 cal/mg, and for anchovy lipid, 9.227 cal/mg. For example, northern anchovy larvae weighing 25 μg contained 6 μg of lipid (unpubl. data: John Hakanson, UCSD, Scripps Institution of Oceanography); using the above caloric equivalents for 19 μg of fat-free tissue and 6 μg of lipid yields 5.36 cal/mg as the energy equivalent of anchovy tissue. In a 20-d laboratory experiment, Hakanson found that lipid weight appeared to increase proportionally with anchovy weight, thus the caloric content of anchovy tissue would be approximately constant for the age range studied. Lipid content seems to be lower in older northern anchovy larvae. The only other information I found was for 40-60 d-old northern anchovy where the caloric content averaged 4.9 cal/mg (unpubl. data: John Hunter, Southwest Fisheries Center). I used 5.4 cal/mg as the caloric value of anchovy tissue for larvae between 5 and 14 days of age.

Evacuation

Gut clearance times were determined for actively feeding fish of various ages fed the rotifer and copepods diets. Larvae were transferred from the 100 L rearing tank to a 10 L test tank. Because northern anchovy larvae are sensitive to handling, handling was restricted to one transfer. Transferred larvae were kept in the test tank for 18 hours prior to an evacuation experiment because injured larvae usually die within 8-10 hours after transfer. First, larvae were fed a low concentration of prey that had been dyed with National Fast Blue (Laurence 1971). After larvae had filled their guts, eating most of the dyed prey, a known density of undyed prey was added. Larvae were sampled at 5-min intervals, and the time required for them to void their guts of the dyed prey was determined. The number of prey in the full guts was counted and converted to dry weight. Evacuation rates are given as μg prey cleared through the gut per hour. Rates were related to fish size and to prey type.

TABLE 5.—Parameters for equation $Q = aw^b$ where Q is metabolic rate in $\mu\text{L O}_2/\text{h}$ for northern anchovy and w is its fresh dry weight.

Model	N	Size group (mg dry wt) w	Parameters	
			a (SE)	b (SE)
1	89	0.02-2.70	13.844 ± 0.100	0.858 ± 0.029
2	72	0.02-0.14	2.897 ± 0.344	0.834 ± 0.057
2	17	0.14-2.70	4.269 ± 0.325	0.697 ± 0.107

¹The sum of the residuals in Model 1 does not equal zero, thus the program calculation of SE's is biased.

The timing of the second prey addition was not critical for determining gut clearance rates at high prey densities. But when the timing was not correct for the tests that used low prey concentrations, deciphering the meaning of the gut contents was problematical. Results from most of these low-density tests could not be used.

A series of evacuation experiments also was conducted with nonfeeding northern anchovy that were removed from their food source, rotifers, to filtered seawater.

To reduce the incidence of injury during transfer, I constructed a cylindrical, clear plastic container (15 mm high and 7 mm diameter) with handle and a removable bottom grooved to fit the circumference of the cylinder. Larvae to be transferred were surrounded by the cylinder, and then the bottom was fitted onto the cylinder. The container with fish was transferred and lowered into the test tank. Removing the bottom and slowly raising the cylinder released the fish. Prey that were transferred into the experimental tank with the larvae were removed by an air-lift pump that slowly recirculated water and was screened to prevent the removal of larvae (O'Connell and Paloma 1981).

Growth Efficiency

To determine growth efficiencies, I used the information on growth (Table 4), daily food consumption estimated from the general equations (Table 3) and evacuation rates of 1.15 hours for the high-density rotifer diet and 1.5 hours for the low-density diet. Gross growth efficiency was estimated based on dry weight and on caloric estimates. It is the ratio of growth to ingestion. To estimate assimilation efficiency, I used the information on weight-specific metabolic rates and simply combined the energy of metabolism and growth and divided it by the energy

consumed. Assimilated energy lost as feces and urine was not accounted for.

RESULTS

Feeding

Sizes of prey fed to larval northern anchovy in these experiments ranged from 50 μ m for *Gymnodinium*, to 74-195 μ m for rotifers and copepod nauplii, and 147-221 μ m for copepodites. In contrast to larvae fed the rotifer diets, fish offered the copepod diet did not switch from eating *Gymnodinium* at first feeding on day 3 to eating larger prey on day 5. All fish fed copepods and sampled on day 5 contained *Gymnodinium* in their gut, and 96% of these guts were full of *Gymnodinium* (Table 6). By day 7, the number of copepod-fed northern anchovy eating *Gymnodinium* had decreased to 80%, with 10% full. These data reveal that young northern anchovy were unsuccessful at capturing *Tigriopus* nauplii at 1/mL until 7-8 days of age, and because of this behavior and the failure of the copepod culture on day 9, I was unable to quantify daily consumption for northern anchovy fed copepods.

Northern anchovy reared on the low-density (2/mL) and high-density (25/mL) rotifer diets ate only a few *Gymnodinium* cells after day 4. Between rotifer treatments, incidence of feeding on *Gymnodinium* after day 4 was higher for fish fed the low-density diet (Table 6). On day 5, northern anchovy concentrated on eating rotifers in the 75-150 μ m size range; between 84 and 97% of the rotifers eaten by larvae sampled from both rotifer treatments were <150 μ m width (Table 7). Only 7% of the rotifers available to these larvae were smaller than 150 μ m width. Hence on day 5 larvae were selecting small rotifers in higher proportions than were available; in the two treatments, the apparent density of roti-

TABLE 6.—Presence of *Gymnodinium* in guts of larval northern anchovy related to age of larvae and to diet.

		Diets							
		Rotifers 25/mL ¹				Rotifers 2/mL ²		Copepods 2/mL ³	
Age (d)	<i>n</i>	Incidence (%) ⁴	Gut full (%) ⁵	<i>n</i>	Incidence (%) ⁴	Gut full (%) ⁵	<i>n</i>	Incidence (%) ⁴	Gut full (%) ⁵
5	21	48	0	29	83	0	27	100	96
6	82	59	0	11	9	0	57	77	16
7	10	10	0	5	0	0	49	80	10
8	75	9	0	0	—	—	5	0	0
9	27	7	0	38	6	0	33	0	0

¹Apparent density of rotifers <150 μ m = 2/mL.
²Apparent density of rotifers <150 μ m = 0.1/mL.
³Apparent density of nauplii <150 μ m = 1/mL.
⁴Percent of larvae having *Gymnodinium* cells in guts with rotifers or copepods
⁵Percent of larvae having guts full with *Gymnodinium* cells.

TABLE 7.—Width frequency of prey eaten by northern anchovy (*n*) related to their diets and to their age and size.

Age (d)	Rotifers 25/mL ¹ Prey composition (%)			Rotifers 2/mL ² Prey composition (%)			Copepods 2/mL ³ Prey composition (%)		
	<i>n</i>	<150 μ m	>150 μ m	<i>n</i>	<150 μ m	>150 μ m	<i>n</i>	<150 μ m	>150 μ m
5	21	83.5	16.5	29	97.3	2.7	27	88.0	12.0
6	82	11.0	89.0	11	75.0	25.0	57	60.0	40.0
7	10	5.2	94.8	5	38.7	61.3	49	59.0	41.0
8	75	33.1	66.9	0	—	—	5	33.4	56.6
9	27	40.9	59.1	38	12.2	87.8	33	31.8	68.2
Length (mm)									
4.1-4.5	60	49.7	50.3	37	91.4	8.6	21	80.0	20.0
4.6-5.0	77	25.7	74.3	20	23.4	76.6	69	68.3	13.7
5.1-5.5	55	43.9	56.1	23	15.1	84.9	45	57.3	42.7
5.6-6.0	35	36.6	63.4	9	11.8	88.2	30	40.0	60.0
6.1-6.5	23	38.2	61.8	0	—	—	17	36.4	63.6

¹Apparent density of prey <150 μ m = 2/mL.²Apparent density of prey <150 μ m = 0.1/mL.³Apparent density of prey <150 μ m = 1/mL.

fers <150 μ m was equivalent to about 2 and 0.1/mL. In sum, the larvae switched to eating prey >150 μ m on day 6 in the high-density rotifer treatment, day 7 in the low-density treatment, and day 8 in the copepod treatment (Table 7). If the analysis is based on larval size instead of larval age, selection for prey >150 μ m occurs at 4.6-5.0 mm for northern anchovy fed the rotifer diets and at 5.6-6.0 mm for those fed the copepod diet (Table 7; Fig. 1).

Feeding intensity was highly variable on all diets. The observed stomach contents can differ by as much as a factor of three (Fig. 2) from the predicted stomach contents (C_{max}) used in the feeding models.

At high rotifer densities, northern anchovy filled their guts at a faster rate and consumed more. On average, fish eating the high-density rotifer diet were full within 2 hours, while those eating a low-density diet were full in about 3 hours. Comparing the average observed stomach contents, and excluding empty stomachs, for fish of equal age shows that all larvae eating at the high prey density ate more than their counterparts eating at lower prey densities (Table 8).

Growth

Hunter (1976) showed that the length-weight rela-

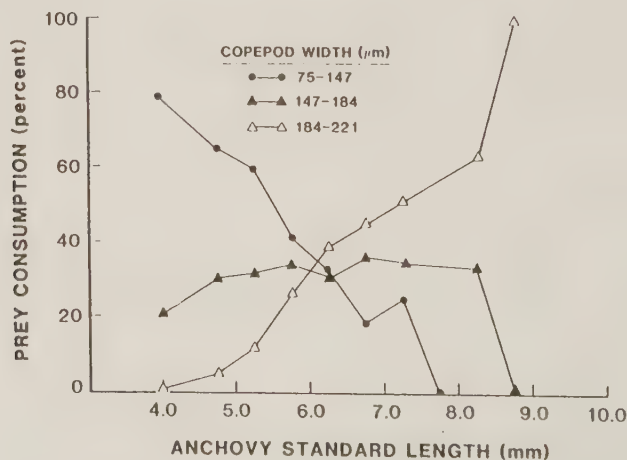


FIGURE 1.—Size of copepod prey eaten by northern anchovy related to fish size. See Table 1 for copepod width classes.

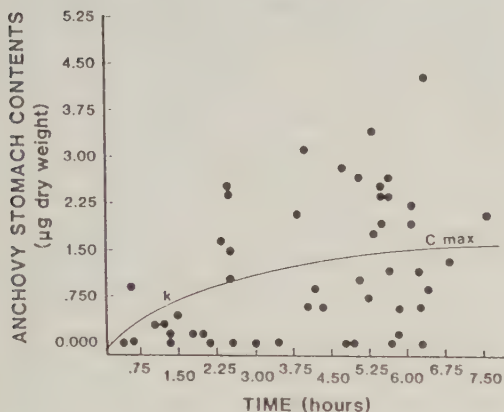


FIGURE 2.—Observed stomach contents of 4.0-4.5 mm northern anchovy fed 25 rotifers/mL, predicted rate of gut filling k and predicted maximum gut content C_{max} . Each point is one larva.

TABLE 8.—Mean dry weight of food (μg) observed in stomachs¹ of northern anchovy (n) related to their age.

Age (d)	Rotifers 25/mL		Rotifers 2/mL		Copepods 2/mL		Copepods 0.2/mL	
	n	μg	n	μg	n	μg	n	μg
5	9	1.75	17	0.60	8	0.18		
6	57	2.23	4	0.27	39	0.55		
7	8	3.56	5	1.41	37	0.67		
8	51	2.10	—	—	3	0.87	1	0.08
9	26	2.99	27	2.60	31	1.88	6	0.78
10	—	—	—	—	—	—	9	1.51
11	6	3.60	—	—	—	—	9	0.42
12	22	5.14	4	26.39	—	—	3	0.90

¹ Average stomach contents (excludes empty stomachs) calculated for $t = >3$ hours; 3 hours is a reasonable time for northern anchovy to fill guts eating at lowest prey densities tested (see text)

² Day 13.

tion for northern anchovy was curvilinear on a log-log plot, and he used a Laird Gompertz model to describe both growth in length and in weight over 75 days. Because I am describing only the first 2 weeks of growth, I used a simpler exponential model (Table 4) which probably should not be used for larvae beyond 2 weeks of age.

Larvae grew at 0.35 mm/day on the copepod diet ($k = 0.07$) and at 0.33 and 0.25 mm/day on the high ($k = 0.06$) and low-density ($k = 0.05$) rotifer diets (Table 4). On the average, the dry weight of larval northern anchovy was proportional to length to the third power. Depending on diet, the length exponent ranged from 2.80 to 3.16 (Table 4).

Daily percent increases in dry weight for northern anchovy fed the rotifer diets were 15% for larvae fed 2/mL and 21% for larvae fed 25/mL. However, northern anchovy grew the most, 23% per day, on the 2/mL copepod diet. For the three diets tested, daily growth in dry weight as a percent was constant over the size range.

An analysis of covariance was used to test for diet-induced differences in the relation between natural logarithms of length and weight for larval northern anchovy between days 5 and 9 when prey concentrations were controlled. Larvae which fed on copepods were significantly longer and heavier at age than larvae eating rotifers. There were no length or weight differences at age 7 days between the two rotifer treatments (Table 9), but there were differences in growth thereafter. Larvae raised on the two rotifer diets were the same weight at 4.9 mm (30.75 and 33.25 μg ; $P = 0.3$), but larvae raised on copepods weighed less at 4.9 mm (28.54 μg) than larvae fed on the rotifer diets ($P = 0.11$ and <0.01).

I compared the distribution of my northern anchovy dry weights at length for the rotifer and

TABLE 9.—Effect of diet on northern anchovy standard length (SL) and dry weight (W).

Diet	Density per mL	No. cases ¹	Age = 7 days		Probabilities = SL and = W		
			$\bar{x}$ SL (mm)	$\bar{x}$ W (μg)	1 vs. 2 SL/W	1 vs. 3 SL/W	2 vs. 3 SL/W
1-Rotifers	25	34	4.78	28.36	0.20/0.71	0.00/0.00	0.00/0.00
2-Rotifers	2	14	4.61	27.33			
3-Copepods	2	28	5.28	35.11			
Diet	Density per mL	No. cases ¹	SL = 4.9 mm		Probabilities		
			$\bar{x}$ W (μg)		1 vs. 2	1 vs. 3	2 vs. 3
1-Rotifers	25	34	30.75		0.30	0.11	0.00
2-Rotifers	2	14	33.25				
3-Copepods	2	28	28.54				

¹ Case numbers contain 2-12 larvae depending on number in group that were weighed.

copepod diets with those in a study by Hunter (1976) where northern anchovy were fed *Brachionus*, 50-100/mL, and copepods, *Tisbe* 0.01/mL, at 17°C and *Gymnodinium* was fed as the first food. The curves show that among experiments there appear to be diet-induced differences in weight at length (Fig. 3).

Metabolism

The caloric equivalent of metabolism for northern anchovy larvae ranging in age from first feeding to 25 days was determined using the relation between the metabolic rate and fresh dry weight (Model 2, Table 5) and by converting the oxygen uptake to calories using an oxycaloric equivalent of 0.00463 cal/ μ L O₂ (Brett and Groves 1979). I assume the metabolic rate approximates "routine" metabolism.

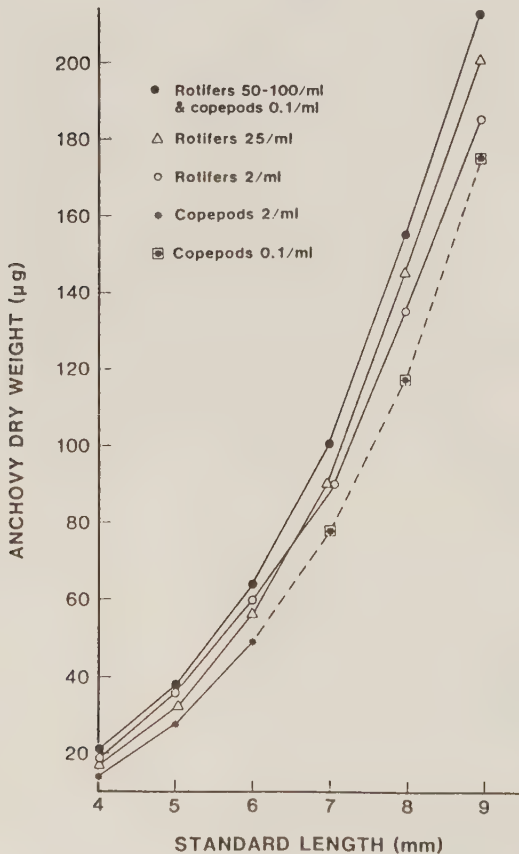


FIGURE 3.—Relation between dry weight and standard length for northern anchovy fed several diets where *Gymnodinium* was the first food.

I also determined the caloric equivalent of metabolism for first-feeding northern anchovy by starving them, determining the weight loss, and converting the loss to calories. Starving larvae lost an average of 10% of their body weight per day for 3 days, after which larvae must have continued to lose weight, but no decrease could be measured (Fig. 4). The time to maximum weight loss was 3-4 days, the time of irreversible starvation for northern anchovy from the onset of feeding (Lasker et al. 1970; Theilacker and Dorsey 1980). Larvae that weighed an average of 0.0211 mg at 3 days of age weighed an average of 0.0148 mg on day 6. The weight loss (0.0063 mg) $\times$ 5.4 cal/mg, which is the assumed caloric equivalent for northern anchovy tissue, equals 0.0339 calories, or a metabolic demand of 0.011 cal/day. This value, determined at a slightly lower temperature, corresponds well with the value obtained for first-feeding northern anchovy weighing 0.0211 mg using respiration measurements (0.013 cal/day).

Evacuation Rates

Gut clearance times for northern anchovy larvae appeared to be independent of larval age; however, the weight of food evacuated per hour increased with age because the stomach contents increased. Because the larvae fed at a constant rate after the gut was filled and defecated continuously, the gut clearance rate for actively feeding northern anchovy larvae was constant. The average gut clearance time for anchovy feeding on 25 rotifers/mL was 1.15 hours (SE = 0.13; range 0.7-1.5 hours; n = 6 tests). Reducing the prey density to 2/mL increased the average gut clearance time to 1.5 hours (range 1.2-1.8 hours; n = 2 tests) for the rotifer diet and 2.73 hours (SE = 0.26; range 2.0-3.3 hours; n = 4 tests) for the copepod diet.

Nonfeeding northern anchovy cleared their guts in 2.8-5.8 hours, depending on their size and stomach capacity (2.8 h/4.8 mm; 4 h/6.3 mm; 5 h/7.9 mm; 5.8 h/8.5 mm).

Daily Consumption of Rotifers and Growth Efficiency

Daily consumption was less on the low-density diet and, as a percent of body weight eaten per day, consumption ranged between 31 and 86%, depending on prey concentration and fish size (Tables 10, 11). For both rotifer diets, weight-specific consumption decreased with increasing body weight (Fig. 5).

Gross growth efficiencies were higher for north-

ern anchovy fed the low-density diet (Tables 10, 11). Mean gross-growth efficiency (days 5-14) based on dry weight was 0.30 for the high-density diet and

0.37 for the low-density diet. Based on calories, mean gross-growth efficiencies were 0.37 and 0.46 respectively.

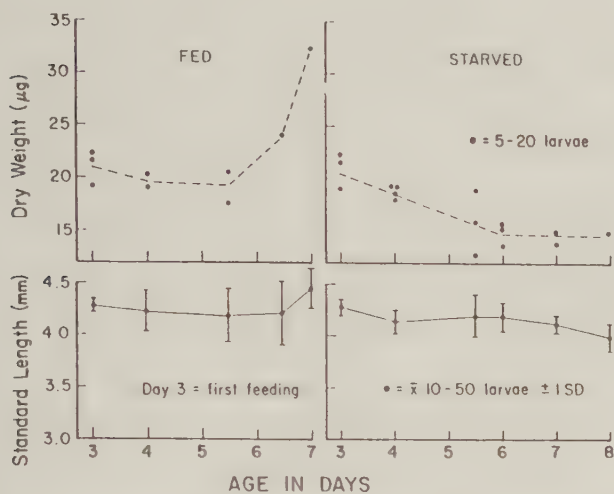


FIGURE 4.—Changes in standard length and weight of fed and starved northern anchovy larvae over time.

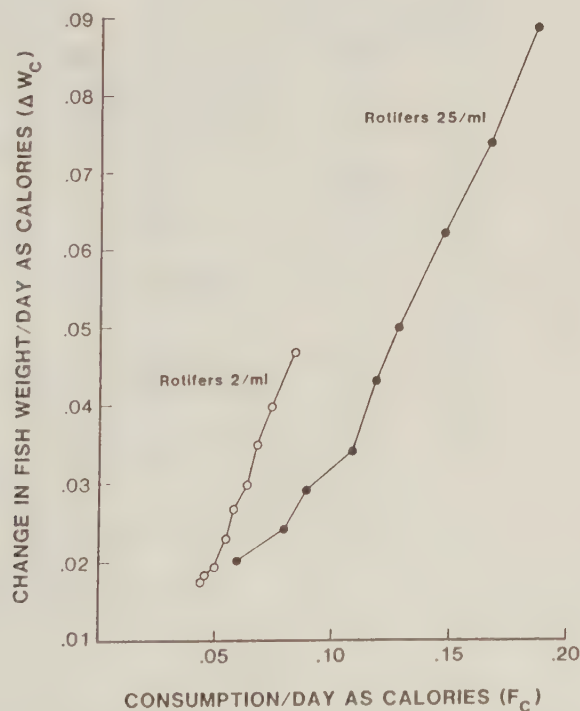


FIGURE 5.—Gross growth efficiencies (W_c/F_c ; Tables 10, 11) of northern anchovy fed rotifers at 25/mL and at 2/mL.

TABLE 10.—Estimation of growth efficiency of larval northern anchovy fed rotifers at 25/mL.

	(1)	(2)	(3)	(4)	(5)			(6)			(7)	(8)	(9)	(10)	(11)	(12)	(13)	(14)	(15)	(16)
	Age (d)	Standard length (mm)	Dry weight (μ g)	Gut clearance rate (μ g/h)	Gut contents		Residual at end of feeding (μ g)	Consumption			Metabolic rate (μ L O ₂ /d) (cal/d)	Change in fish weight (μ g/d) (cal/d)		Gross efficiency		Assimi- lation estimate P				
					Daily mean (μ g)	$\bar{c}$		Food (μ g) F_w	Body weight (%/d) $F_{w/w}$	Calories (cal/d) F_c		ΔW	ΔW_c	$\Delta W/F_w$	$\Delta W_c/F_c$					
Diet	A	I	W	r	$\bar{c}$	C ₁₂	F_w	$F_{w/w}$	F_c	Q_m	ΔW	ΔW_c	$\Delta W/F_w$	$\Delta W_c/F_c$	P					
Rotifers (25/mL)	5	4.13	17.41	1.03	1.19	1.73	14.14	81	0.06	2.36	3.71	0.020	0.26	0.33	50.2					
	6	4.39	21.12	1.34	1.54	2.00	18.11	86	0.08	2.77	4.38	0.024	0.24	0.30	44.4					
	7	4.66	25.50	1.58	1.82	2.19	21.14	83	0.09	3.24	5.35	0.029	0.25	0.32	47.5					
	8	4.95	30.86	1.80	2.07	2.39	23.99	78	0.11	3.80	6.31	0.034	0.26	0.31	45.7					
	9	5.25	37.17	2.03	2.33	2.61	26.97	73	0.12	4.44	7.89	0.043	0.29	0.36	51.3					
	10	5.58	45.06	2.28	2.62	2.88	30.23	67	0.13	5.21	9.27	0.050	0.31	0.38	55.6					
	11	5.92	54.33	2.55	2.94	3.17	33.82	62	0.15	6.09	11.48	0.062	0.34	0.41	58.7					
	12	6.29	65.80	2.88	3.31	3.53	38.04	58	0.17	7.14	13.77	0.074	0.36	0.44	61.7					
	13	6.68	79.57	3.25	3.74	3.96	42.94	54	0.19	8.37	16.48	0.089	0.38	0.47	65.7					
	14	7.09	96.05	3.68	4.24	4.45	48.67	51	0.21	9.79	0.042									

¹Hatching = Day 0.² $l_t = 3.05 e^{0.06t}$, live length.³ $W = 0.197 t^{3.15}$ (on day consumption is estimated); fresh dry weight.⁴ $r = \bar{c}(1.15 \text{ h} - e^{-rt})/12 \cdot dt$.⁵ $\bar{c} = \int_0^{12} C_{\max}(1 - e^{-rt})/12 \cdot dt$.⁶ $C_{12} = C_{\max}(1 - e^{-12k})$.⁷ $F_w = rt + C_{12}$; $t = 12 \text{ h}$.⁸ $F_{w/w}$ ⁹ $F_c = F_w \times 4.4 \text{ cal/mg}$ (see Table 1).¹⁰ $\mu\text{L O}_2/\text{d} = 24 (2.879 W^{0.834})$ (see Table 5).¹¹ $O_m = 0.00463 \times \mu\text{L O}_2/\text{d}$; ($1 \mu\text{L O}_2 = 0.00463 \text{ cal}$) (see text).¹² ΔW = weight gained 1 day after consumption estimated.¹³ $\Delta W_c = \Delta W \times 5.4 \text{ cal/mg}$ (caloric estimation for larva) (see text).¹⁴ $\Delta W/F_w$ ¹⁵ $\Delta W_c/F_c$ ¹⁶ $P = \frac{Q_m + \Delta W_c}{F_c}$

TABLE 11.—Estimation of growth efficiency of larval northern anchovy fed rotifers at 2/mL.

Diet	Age (d)	(1)	(2)	(3)	(4)	Gut contents			Consumption				(10)	(11)	(12)	(13)	(14)	(15)	(16)					
						Standard length (mm)	Dry weight (μg)	Gut clearance rate (μg/h)	Residual at end of feeding (μg)	Food (μg)	Body weight (%d)	Calories (cal/d)								Metabolic rate (μL O ₂ /d)	Change in fish weight (μg/d)	(cal/d)	Gross efficiency	Assimi- lation estimate
Rotifers																								
	5	4.03	18.77	0.72	1.08	1.23	1.23	9.87	53	0.043	2.50	0.012	2.87	0.015	0.29	0.35	67.3							
	6	4.24	21.64	0.76	1.15	1.31	1.31	10.51	49	0.046	2.83	0.013	3.29	0.018	0.31	0.39	66.6							
	7	4.46	24.93	0.83	1.24	1.41	1.41	11.33	45	0.050	3.18	0.015	3.60	0.019	0.32	0.38	68.4							
	8	4.68	28.53	0.89	1.33	1.52	1.52	12.16	43	0.054	3.56	0.016	4.29	0.023	0.35	0.43	74.0							
	9	4.92	32.82	0.96	1.44	1.64	1.64	13.16	40	0.058	4.00	0.019	5.09	0.027	0.39	0.47	79.3							
	10	5.18	37.19	1.05	1.57	1.79	1.79	14.35	38	0.063	4.51	0.021	5.57	0.030	0.39	0.47	79.3							
	11	5.44	43.48	1.14	1.71	1.94	1.94	15.62	36	0.069	5.06	0.023	6.56	0.035	0.42	0.51	85.5							
	12	5.72	50.04	1.25	1.87	2.13	2.13	17.09	34	0.075	5.68	0.026	7.44	0.040	0.44	0.53	88.3							
	13	6.01	57.48	1.37	2.06	2.34	2.34	18.82	33	0.083	6.38	0.030	8.69	0.047	0.46	0.57	92.2							
	14	6.32	66.17	1.52	2.28	2.59	2.59	20.83	31	0.092	7.18	0.033												

¹Hatching = Day 0.² $l_t = 3.14 e^{0.05t}$; live length.³ $W = 0.379 t^{2.80}$ (on day consumption is estimated); fresh dry weight.⁴ $r = \bar{C}/1.5$ h (see text).⁵ $\bar{C} = \int_0^{12} C_{\max} (1 - e^{-kt})/12 dt$.⁶ $C_{12} = C_{\max} (1 - e^{-12k})$.⁷ $F_w = r t + C_{12}$; $t = 12$ h.⁸ $F_w = W$.⁹ $F_c = F_w \times 4.4$ cal/mg (see Table 1).¹⁰ $\mu\text{L O}_2/\text{d} = 24 (2.879 W^{0.834})$ (see Table 5).¹¹ $Q_m = 0.00463 \times \mu\text{L O}_2/\text{d}$; ($1 \mu\text{L O}_2 = 0.00463$ cal) (see text).¹² $\Delta W =$ weight gained 1 day after consumption estimated.¹³ $\Delta W_c = \Delta W \times 5.4$ cal/mg (caloric estimation for larva) (see text).¹⁴ $\Delta W/F_w$.¹⁵ $\Delta W_c/F_c$.¹⁶ $P = \frac{Q_m + \Delta W_c}{F_c}$.

DISCUSSION

Larval northern anchovy feeding ecology was similar to other larval fishes (Laurence 1977; Haegler and Outran 1978; Werner and Blaxter 1980; Theilacker and Dorsey 1980; Blaxter and Hunter 1982; Eldridge et al. 1982; Houde and Schekter 1981, 1983). As the larval northern anchovy grew they selected increasing larger prey, and on the rotifer diets, their feeding and growth rates increased with increasing concentrations of prey. In addition to the growth response to different prey concentrations, I observed differences in growth due to prey type. Fish grew the fastest on the copepod diet where one-third fewer calories were available than were available in the high-density rotifer diet (4×10^{-2} vs. 13×10^{-2} cal/mL for prey $<150 \mu\text{m}$).

Length at age obtained for the first 2 weeks by larvae raised on copepods agreed with previous studies where northern anchovy were fed copepods and *Gymnodinium* was the first food (Kramer and Zweifel 1970; Hunter 1976). However, the larvae raised on copepods did not put on as much weight per unit length as their counterparts fed rotifers and *Gymnodinium*. Between days 5 and 9, the faster growing, copepod-fed larvae had significantly lower size-specific weights, and the weight exponents estimated for the first 2 weeks were lower, 2.9, than for larvae feeding on the high-density rotifer diet, 3.2. Lasker et al. (1970) found an exponent of 3.3 for northern anchovy fed on a high-density veliger and *Gymnodinium* diet.

These weight exponents estimated for northern anchovy are lower than the exponents of about 4 reported for deep-bodied fish larvae (haddock, flounder, cod, and scup; Laurence 1979). Likewise the exponents obtained for Atlantic herring ranged between 3.8 and 4.7 (reviewed by Checkley 1984). Weights of fishes used to estimate the exponents in the other laboratory studies ranged between 20 and 10,000 μg , whereas the northern anchovy weights ranged between 20 and 100 μg . Differences in growth rates occur as larval fish grow (Zweifel and Lasker 1976), and length-weight relations may change over the size range. Additionally, larval morphology is an obvious important component in the length-weight relation, and experimental variables may further complicate the relation. Moksness (1982) reported a low weight exponent of 2.6 for capelin, *Mallotus villosus*, from the field and from a large rearing basin. Both Atlantic herring and capelin larvae are similar in morphology to northern anchovy.

In previous laboratory feeding studies of larval

northern anchovy, percent of body weight eaten per day was usually higher than consumption rates, 31-86%, I estimated. Reported values were 126-144% for northern anchovy (Hunter 1972), 197-440% for bigeye anchovy (Chitty 1981), and 20-295% for bay anchovy (Houde and Schekter 1981). Consumption varies with prey concentration and temperature, and the differences may be due to the experimental conditions. In the other studies, temperatures were higher and food concentrations were both lower and higher, with some including *Chlorella* blooms. However, it is likely that the differences are due to use of average food weights in the other studies. First-feeding northern anchovy larvae select small prey (Table 7; Fig. 1), and if average prey weight is larger than those actually being eaten by the larvae, their consumption may have been overestimated. For example, in Table 2, the average full stomach (C_{max}) of 4.25 mm fish (day 4-5) fed 25 rotifers/mL contained 15.55 rotifers while the average 4.75 mm fish (day 5-6) contained 7.79 rotifers. Using the width-specific weights (Table 1), I converted the 15 small rotifers to 1.8 μg and the 8 larger ones to 2.1 μg .

The exponent for the regression relating oxygen consumption to northern anchovy weight was 0.834 for larvae weighing <0.14 mg and 0.697 for larger larvae. Exponents have been reported for larval winter flounder, *Pseudopleuronectes americanus* (0.74; Laurence 1975); larval bay anchovy, *Anchoa mitchilli* (0.8; Houde and Schekter 1983); larval sea bream, *Archosargus rhomboidalis*, and larval lined sole, *Achirus lineatus* (0.838 and 0.942; Houde and Schekter 1983). Brett and Groves (1979) suggested a weight exponent of 0.86 for adult fish. There is considerable variation in respiration rates in the literature, probably depending on experimental conditions. The respiration rates given here for northern anchovy range between 3.1 and 6.9 $\mu\text{L}/\text{mg}$ per hour for 0.02-2.7 mg larvae, and they are comparable to rates given for other fishes of similar age and size (reviewed by Theilacker and Dorsey 1980).

The evacuation rates determined here, 1.15-2.73 hours, for actively feeding northern anchovy larvae are comparable to rates of 1-3 hours estimated by Arthur (1976) for field samples. Particle residence time in the gut depended on prey density, prey type, and experimental design, e.g., feeding vs. nonfeeding larvae. Werner and Blaxter (1980) also showed that evacuation rates for herring fed *Artemia* were more rapid at higher prey densities, and because live and undigested prey were defecated, assimilation must have been low at these high prey densities.

Northern anchovy larvae, like herring, are con-

tinuous feeders, and at the high prey concentration, high consumption rates reduced the gut residence time and decreased digestion (assimilation; Tables 10, 11). At the lower prey concentration, the slower digestion time and increase in assimilation was not sufficient to compensate for the reduced consumption, and daily increase in weight, 15%, was less than the weight increase on the high-density diet, 21%. This result is similar to that in the recent study on assimilation by Pacific herring larvae fed *Brachionus* and *Artemia* (Boehlert and Yoklavich 1984). Using radioisotope tracers, Boehlert and Yoklavich found decreased assimilation at high food densities, but overall the larvae had a greater total energy gain at the high food densities because the higher food consumption more than compensated for the decreased assimilation.

Assimilation estimates, given here for northern anchovy larvae, fed two rotifer diets, averaged 53 and 79% and are somewhat higher than rates of 39-68%, depending on prey density, given by Boehlert and Yoklavich (1984) for Pacific herring. The assimilation estimates for northern anchovy larvae may not be reliable because the estimate assumes that weight-specific metabolic rates of fish fed both diets were equal. In addition, I made no attempt to correct for activity or to partition the portion of food assimilated into parts lost as feces and urine. Buckley and Dillman (1982) developed a technique to measure nitrogenous wastes of larval flounder. Assimilation efficiencies of 65-75% are commonly used in calculations of larval fish growth efficiencies (Ware 1975).

Estimates of gross growth efficiencies are not compromised by the above concerns. Larval northern anchovy gross-growth efficiencies increased with age, indicating that an increasing fraction of the calories consumed was translated into growth (Tables 10, 11). It is unrealistic that growth efficiencies would continue to increase. Brett and Groves (1979) suggested that for older fish growth rates become asymptotic with time. Growth efficiencies given here (24-46%) are consistent with growth efficiencies reported for other larval fish species (14-41% in Theilacker and Dorsey 1980) fed 1,000 or more prey per liter; reported efficiencies are high and extremely variable.

Direct observations of larval stomach contents showed that some rotifer-fed larvae fed at three times the average rate (C_{max} ; Fig. 2). These fish may be the successful ones that survive in the field. Their high feeding rates would yield faster growth through the vulnerable larval stage. Feeding intensity also was highly variable for larvae eating cope-

pods (Fig. 6), but the average number of copepods eaten was less than the average number of rotifers eaten (Table 2).

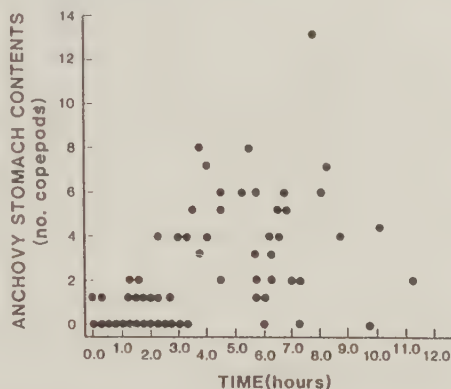


FIGURE 6.—Number of copepod nauplii observed in stomachs of 4.0-5.0 mm northern anchovy fed 2 copepods/mL. Each point is one larva.

Northern anchovy raised on copepods ate mainly *Gymnodinium*, augmenting their diet with copepod nauplii (Table 12). The stomachs of 96% of the 5-d-old larvae were full with *Gymnodinium* cells (Table 6). Fish were obtaining 60-90% of their daily caloric intake from *Gymnodinium*. This is evident by comparing the daily caloric intake (F_c) for day 5-6 larvae of equal size or weight that were fed copepods (Table 12) with those fed rotifers (Tables 10, 11). Consumption of 2-4 cells/minute can account for this energy input (4.2×10^{-5} cal/*Gymnodinium* cell [Vlymen 1977]), and successful feeding acts of this magnitude have been directly observed by Hunter (1981). Lasker and Zweifel (1978) developed a model (a modified version of Vlymen's [1977] model) to describe survival at sea in areas of various concentrations and proportions of large and small prey and concluded that large prey made very little contribution to survival of first-feeding larvae when sufficient (40 mL) small prey were available. As observed here, the ingestion of 10-20 copepod nauplii/day in addition to small *Gymnodinium* cells resulted in a growth rate of 0.35 mm/day, which is comparable to a rate of 0.37 mm/day reported for wild northern anchovy of similar age (Methot and Kramer 1979), and lends additional credence to Lasker and Zweifel's (1978) hypothesis that survival of northern anchovy depends on patchy (layered) distributions of small, abundant prey like *Gymnodinium*.

For all diets, an equivalent number of small prey,

TABLE 12.—Estimate of caloric input from copepods eaten by northern anchovy.

Diet	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)
	Age (d)	Standard length (mm)	Dry weight (μ g)	Gut clearance rate (μ g/h)	Gut contents		Consumption		
					Daily mean (μ g)	Copepods (μ g)	Body weight (%/d)	Copepods (cal/d)	
	A	I	W	r	$\bar{c}$ est	$\bar{c}$ obs	F_w	$F_{w/W}$	F_c
Copepods	5	4.34	20.35	0.07	0.19	0.16	1.07	05	0.0052
2/mL	6	4.66	24.99	0.10	0.28	0.30	1.55	06	0.0076
and	7	4.99	30.43	0.15	0.41	0.43	2.26	07	0.0111
<i>Gymnodinium</i>	8	5.36	37.39	0.23	0.62	0.68	3.44	09	0.0169
	9	5.75	45.77	0.35	0.96	1.08	5.32	12	0.0261

¹Hatching = Day 0.² $r_i = 3.06 e^{0.071}$.³ $W = 0.297 I^{2.88}$.⁴ $r = \bar{c}$ est/2.73 h (see text).⁵Estimated using equation in Table 3.⁶Average stomach contents calculated for $t = >3$ h; includes empty stomachs.⁷ $F_w = 12 r + \bar{c}$ est.⁸% body weight eaten/d as copepods.⁹Calories/d, copepods; $F_w \times 4.9$ cal/mg (Table 1).

Gymnodinium cells, was available and the concentration of large prey was varied. Availability of large prey of a suitable size in the copepod diet was 10 times the number available in the low-density rotifer diet. Because 4 mm (day 5) larvae fed copepods ate mainly *Gymnodinium*, and those fed the low-density rotifer diet ate mainly rotifers (Tables 2, 6), copepods nauplii must be more difficult to catch than rotifers, and consequently larvae consumed the more abundant *Gymnodinium* cells. Larvae which consume prey as they are encountered, rather than choosing a diet that maximizes the energy gained per unit foraging time, have been labelled "number maximizers" as opposed to "energy maximizer" in the parlance of Griffiths (1975) and Hughes (1979). Additional evidence that points to northern anchovy feeding as "number maximizers" is that, when prey of the proper size were available, their feeding rates paralleled prey abundance (Tables 10, 11).

The energy budget I calculated for northern anchovy fed rotifers at two concentrations gives information on their growth requirements that can be translated to growth requirements in the field. My data support Boehlert and Yoklavich's (1984) and Checkley's (1984) conclusions that larval fish may exhibit a high growth rate or a high growth efficiency, but not both at the same time. Boehlert and Yoklavich studied Pacific herring, which are 2-4 times the weight of northern anchovy, but like anchovy feed continuously, and found that as consumption increased, the total amount of food assimilated continued to increase despite a decrease in the efficiency of the assimilation. Checkley studied Atlantic herring and found that the gross growth efficiencies of Atlantic herring increased with increasing consumption, but he showed that the relation was peaked, and by incorporating results from the

literature for other species, he also described a decrease in growth efficiency at high consumption for larval fishes.

ACKNOWLEDGMENTS

I wish to thank Patricia Hadley Hansen for her capable assistance during the laboratory phase of this work, Bob Lucas for conducting the evacuation experiments on nonfeeding larvae, Amy Kimball for assisting with the data analysis, and Nancy C. H. Lo for her consultation and valuable suggestions. John Hunter, Pattie Schmitt, Ken Frank, Timothy C. Lambert, and two anonymous referees critically reviewed the manuscript and offered suggestions. I appreciated the help of the manuscript support staff, in particular Jean Michalski and Lorraine Prescott.

LITERATURE CITED

- ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax* and *Trachurus symmetricus*. Fish. Bull., U.S. 74:517-530.
- BEYER, J. E.
1980. Feeding success of clupeoid fish larvae and stochastic thinking. Dana 1:65-91.
- BLAXTER, J. H. S., AND J. R. HUNTER.
1982. The biology of clupeoid fishes. Adv. Mar. Biol. 20:2-223.
- BOEHLERT, G. W., AND M. M. YOKLAVICH.
1984. Carbon assimilation as a function of ingestion rate in larval Pacific herring, *Clupea harengus pallasii*. J. Exp. Mar. Biol. Ecol. 79:251-262.
- BRETT, J. R., AND T. D. D. GROVES.
1979. Physiological energetics. In W. S. Hoar and D. J. Randall (editors), Fish physiology, Vol. 8, p. 279-352. Acad. Press, N.Y. and Lond.

- BUCKLEY, L. J., AND D. W. DILLMANN.
1982. Nitrogen utilization of larval summer flounder, *Paralichthys dentatus* (Linnaeus). J. Exp. Mar. Ecol. 59:243-256.
- CHECKLEY, D. M., JR.
1984. Relation of growth to ingestion for larvae of Atlantic herring, *Clupea harengus* and other fish. Mar. Ecol. Prog. Ser. 18:215-224.
- CHITTY, N.
1981. Behavioural observation of feeding larvae of bay anchovy *Anchoa mitchilli* and big eye anchovy *Anchoa lamprotaenia*. In R. Lasker and K. Sherman (editors), The early life history of fish, p. 320-321. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:320-321.
- ELDRIDGE, M. B., J. A. WHIPPLE, AND M. J. BOWERS.
1982. Bioenergetics and growth of striped bass, *Morone saxatilis*, embryos and larvae. Fish. Bull., U.S. 80:461-474.
- ELLIOTT, J. M., AND L. PERSSON.
1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977-991.
- GRIFFITHS, D.
1975. Prey availability and food of predators. Ecology 56:1209-1214.
- HAEGLER, C. W., AND B. N. OUTRAM.
1978. The effects of diet and ration on the growth and survival of Pacific herring, *Clupea harengus pallasi*, larvae. Fish. Mar. Serv. Tech. Rep. 767, 41 p.
- HOUDE, E. D., AND R. C. SCHEKTER.
1981. Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:441-453.
1983. Oxygen uptake and comparative energetics among eggs and larvae of three subtropical marine fishes. Mar. Biol. 72:283-293.
- HUGHES, R. N.
1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. Am. Nat. 113:209-221.
- HUNTER, J. R.
1972. Swimming and feeding behavior of larval anchovy, *Engraulis mordax*. Fish. Bull., U.S. 70:821-838.
1976. Culture and growth of northern anchovy, *Engraulis mordax*, larvae. Fish. Bull., U.S. 74:81-88.
1977. Behavior and survival of northern anchovy, *Engraulis mordax*, larvae. Calif. Coop. Oceanic Fish. Invest. Rep. 19:138-146.
1981. Feeding ecology and predation of marine fish larvae. In R. Lasker (editor), Marine fish larvae, p. 34-77. Univ. Wash. Press, Seattle and London.
- HUNTER, J. R., AND R. LEONG.
1981. The spawning energetics of female northern anchovy *Engraulis mordax*. Fish. Bull., U.S. 79:215-230.
- JOBLING, M.
1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. J. Fish. Biol. 19:245-257.
- KRAMER, D., AND J. R. ZWEIFEL.
1970. Growth of anchovy larvae (*Engraulis mordax* Girard) in the laboratory as influenced by temperature. Calif. Coop. Oceanic Fish. Invest. Rep. 14:84-87.
- LASKER, R.
1964. An experimental study of the effect of temperature on the incubation time, development and growth of Pacific sardine embryos and larvae. Copeia 1964:399-405.
- LASKER, R., H. M. FEDER, G. H. THEILACKER, AND R. C. MAY.
1970. Feeding growth and survival of *Engraulis mordax* larvae reared in the laboratory. Mar. Biol. 5:345-353.
- LASKER, R., AND J. ZWEIFEL.
1978. Growth and survival of first-feeding northern anchovy larvae (*Engraulis mordax*) in patches containing different proportions of large and small prey. In John H. Steele (editor), Spatial pattern in plankton communities, p. 329-354. Plenum Publ. Corp.
- LAURENCE, G. C.
1971. Digestion rate of larval largemouth bass. New York Fish Game J. 18(1):52-56.
1975. Laboratory growth and metabolism of the winter flounder *Pseudopleuronectes americanus* from hatching through metamorphosis at three temperatures. Mar. Biol. 32:223-229.
1977. A bioenergetic model for the analysis of feeding and survival potential of winter flounder, *Pseudopleuronectes americanus*, larvae during the period from hatching to metamorphosis. Fish. Bull., U.S. 75:529-545.
1979. Larval length-weight relations for seven species of northwest Atlantic fishes reared in the laboratory. Fish. Bull., U.S. 76:890-895.
- LEONG, R.
1971. Induced spawning of the northern anchovy, *Engraulis mordax* Girard. Fish. Bull., U.S. 69:357-360.
- LOVEGROVE, T.
1966. The determination of the dry weight of plankton and the various factors on the values obtained. In H. Barnes (editor), Some contemporary studies in marine science, p. 429-467. Hafner Publ. Co., N.Y.
- METHOT, R. D., AND D. KRAMER.
1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull., U.S. 77:413-423.
- MOFFATT, N. M.
1981. Survival and growth of northern anchovy larvae on low zooplankton densities as affected by the presence of a *Chlorella* bloom. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:475-480.
- MOKSNESS, E.
1982. Food uptake, growth and survival of capelin larvae (*Mallotus villosus muller*) in an outdoor constructed basin. Fiskeridir. Skr. Ser. Havunders. 17:267-285.
- O'CONNELL, C. P., AND PEDRO A. PALOMA.
1981. Histochemical indications of liver glycogen in samples of emaciated and robust larvae of the northern anchovy, *Engraulis mordax*. Fish. Bull., U.S. 79:806-812.
- O'CONNELL, C. P., AND L. P. RAYMOND.
1970. The effect of food density on survival and growth of early post yolk-sac larvae of the northern anchovy (*Engraulis mordax* Girard) in the laboratory. J. Exp. Mar. Biol. Ecol. 5:187-197.
- PEARCY, W. G., G. H. THEILACKER, AND R. LASKER.
1969. Oxygen consumption of *Euphausia pacifica*: The lack of a diel rhythm or light-dark effect, with comparison of experimental techniques. Limnol. Oceanogr. 14:219-223.
- STAUFFER, G. D.
1973. A growth model for salmonids reared in hatchery environments. Ph.D. Thesis, Univ. Washington, Seattle.
- THEILACKER, G. H., AND K. DORSEY.
1980. Larval fish diversity. In Workshop on the effects of environmental variation on the survival of larval pelagic fishes, p. 105-142. Intergov. Oceanogr. Comm. Rep. No. 28. UNESCO, Paris.
- THEILACKER, G. H., AND A. S. KIMBALL.
1984. Comparative quality of rotifers and copepods as foods for larval fishes. Calif. Coop. Oceanic Fish. Invest. Rep. 15:80-86.

- THEILACKER, G. H., AND M. F. MCMASTER.
1971. Mass culture of the rotifer, *Brachionus plicatilis*, and its evaluation as a food for larval anchovies. *Mar. Biol.* 10:183-188.
- VLYMEN, W.
1977. A mathematical model of the relationship between larval anchovy (*E. mordax*), growth, prey microdistribution and larval behavior. *Environ. Biol. Fishes* 2:211-233.
- WARE, D. M.
1975. Relation between egg size, growth and natural mortality of larval fish. *J. Fish. Res. Board Can.* 32:2503-2512.
- WERNER, R. G., AND J. H. S. BLAXTER.
1980. Growth and survival of larval herring (*Clupea harengus*) in relation to prey density. *Can. J. Fish. Aquat. Sci.* 37: 1063-1069.
- ZWEIFEL, J. R., AND R. LASKER.
1976. Prehatch and posthatch growth of fishes—a general model. *Fish. Bull., U.S.* 74:609-621.

Widow Rockfish Fishery

EDWARD UEBER

Southwest Fisheries Center Tiburon Laboratory
National Marine Fisheries Service, NOAA
Tiburon, CA 94920

ABSTRACT

Widow rockfish (*Sebastes entomelas*) was the most important West Coast groundfish species in 1980. Prior to 1978, fishermen sold only limited amounts never exceeding 1,000 MT. This paper predicts that sold landings of widow rockfish will expand to 25,000 MT and account for one-fourth of domestic landings by 1983. The possible reason why widow rockfish were not widely sold prior to 1979, why this fishery has developed and what may occur after 1983 are also discussed.

INTRODUCTION

In 1980 widow rockfish (*Sebastes entomelas*) accounted for 20,000 mt or 45 percent of the estimated 44,000 mt of rockfish landed on the West Coast. Widow rockfish in 1980 was the most important commercial groundfish species, with catches amounting to 22 percent of the 90,000 mt total landings. The current importance of the widow rockfish fishery is surprising since landings had never exceeded 1,000 mt prior to 1978. This paper discusses possible reasons for the lack of earlier development, the current rapid development, and the future of widow rockfish.

ROCKFISH FISHERY

Rockfish, *Sebastes* sp. and *Sebastes* sp., have been part of the domestic groundfish fishery off California, Oregon, and Washington since 1876 (Scofield 1948). Domestic and foreign retained catches of rockfish are given in Table 1. Domestic landings from 1962 to 1975 were fairly constant, averaging 9,800 mt, but the fishery started to expand rapidly in 1976 and landings increased to 44,000 mt in 1980. Estimated foreign catches of rockfish were 44,000 mt in 1967. Following this and other large removals in the late 1960's, an agreement was reached between the United States and the Soviet Union, Japan, and Poland. These international agreements prohibited directed foreign fishing for rockfish, and since the enactment of the Fishery Conservation and Management Act of 1976, both regulation and reduction in foreign fishing have resulted in foreign landings below 1,000 mt.

Increases in domestic landings were caused by changes in the market for fresh rockfish, as well as changes in fishing technology. A major market change was the commencement of sales of rockfish fillets to areas other than the West Coast. Changes in fishing technology have been occurring for years and include high rise nets in 1943 (Scofield 1948), roller gear improvements in 1964 (J. Robinson, Ore. Dep. Fish. Wildl., Newport, OR, pers. commun. 1980) and 1970 (Fisher 1972), single-vessel midwater trawl in 1967

Table 1—U.S. and foreign retained catches of rockfish from California, Oregon, and Washington, 1962-80.

Year	Domestic (1000 mt)	Yearly changes (%)	Foreign (1000 mt)	Total (1000 mt)
1962	12.3	—	—	12.3
1963	12.2	+01	—	12.2
1964	11.2	-08	—	11.2
1965	13.4	+20	—	13.4
1966	10.0	-25	—	10.0
1967	7.0	-30	44.0	51.0
1968	7.5	+07	20.0	27.5
1969	8.2	+09	3.0	11.2
1970	7.5	-09	3.0	10.5
1971	7.5	±00	2.0	9.5
1972	9.2	+23	4.0	13.2
1973	10.5	+14	11.0	21.5
1974	9.5	-10	10.0	19.5
1975	11.3	+19	8.0	19.3
1976	15.6	+38	5.0	20.6
1977	18.2	+17	+	18.3
1978	25.5	+40	+	25.6
1979	27.4	+07	1.0	28.4
1980	44.0	+61	1.0	45.0

Source: Anonymous 1980

(Pereyra and Richards 1970), and advances in electronics which have greatly enhanced detection of fish and precise determination of vessel position.

The expanding rockfish fillet market from 1976 through 1978 stimulated greater landings of traditional rockfish; however, these landings were not sufficient to supply both the old and new markets. This shortfall in supply was a factor in causing the real (deflated) ex-vessel price of rockfish to increase (Table 2). Between 1972 and 1979 the ex-vessel value of rockfish averaged about 32 percent of the total ex-vessel value of the groundfish fishery. The 1980 estimate of the ex-vessel rockfish value accounted for about half of the ex-vessel groundfish fishery value, even though other groundfish landings have also increased. This large increase in rockfish value was due to increases in both landings and ex-vessel prices. The real ex-vessel price had increased about 2 percent per year from \$0.12/kg in 1962 to \$0.21/kg in 1977. In 1978 the real ex-vessel price reached a maximum of \$0.23/kg.

I believe a number of events contributed to the increase in rockfish landings from 1975 through 1978, including:

1. Increases in real ex-vessel rockfish prices from \$0.16/kg in 1975 to \$0.23/kg in 1978 (Fishermen's Marketing Assn., Eureka, CA 95501).
2. Enactment of the Fishery Conservation and Management Act, which many fishermen believed excluded foreign fishing.
3. Increased investments in midwater trawlers built for use in other fisheries but which entered the rockfish fishery.
4. Increased expenses of larger vessels which necessitated greater fishing effort.
5. Expanded markets for fresh rockfish fillets.

However, since 1978 prices have declined to \$0.13/kg in 1980. This was a 43 percent decline in 2 years.

Table 2—Average real and nominal ex-vessel prices for rockfish, and percentage of total ex-vessel value of groundfish attributed to rockfish.

Year	Nominal (¢/kg)	Real (¢/kg)	CPI ¹ 1967 = 100	Total ex-vessel value rockfish/groundfish Percent
1962	11.2	12.3	91.5	n.a.
1963	11.2	12.1	92.9	n.a.
1964	12.3	13.0	94.7	n.a.
1965	12.3	12.8	95.9	n.a.
1966	12.9	13.2	97.1	n.a.
1967	12.9	12.9	100.0	n.a.
1968	12.3	11.8	104.5	n.a.
1969	13.4	12.1	110.2	n.a.
1970	13.4	12.1	110.2	n.a.
1971	14.6	12.5	115.8	n.a.
1972	16.8	13.4	124.3	32
1973	19.0	14.6	131.5	31
1974	25.8	17.7	144.4	30
1975	25.8	16.1	159.1	29
1976	31.4	18.6	168.0	32
1977	38.7	21.3	180.0	37
1978	41.4	22.6	183.0	33
1979	44.8	22.2	210.7	32
1980	33.6	13.4	251.4	49

Source: Anonymous 1980.

¹Consumer Price Index for San Francisco, Bureau of Labor Statistics, U.S. Dep. Labor.

WIDOW ROCKFISH

Yellowtail and canary rockfish (*Sebastes flavidus* and *S. pinniger*, respectively) accounted for most increases in rockfish landings in 1976 and 1977. By 1978, widow rockfish, also called brownies, brown bombers, and soft browns, began being landed in large amounts. Although canary and yellowtail rockfish increases were expansions of previously utilized species, widow rockfish had generally been underutilized.

Substantial domestic utilization of widow rockfish did not occur until 1978 because many processors believed that widow rockfish had several negative characteristics, including:

1. Short shelf life of both fresh and frozen products.
2. Excessive loss of fluid after packaging.
3. Loss of color or a gray color.
4. Unusual smell.
5. Softer flesh than other rockfish.
6. Poor quality of defrosted product.
7. Low fillet yield.

These presupposed characteristics generally kept domestic processors from buying widow rockfish, and prior to 1975 landings were under 1,000 mt. Occasionally during the 1960's, processors did purchase widow rockfish but only in late winter or early spring when inventories of other rockfish were low and demand for rockfish fillets high.

In 1978 a few West Coast fishermen and processors began to experiment with better fishing methods, at-sea preservation, and onshore rapid processing of Pacific whiting. At the same time, fishermen and processors began to use these newly developed techniques to catch, preserve, and process widow rockfish with the result that the widow rockfish did not have the negative characteristics many processors had attributed to this species. Once processors and wholesalers realized widow rockfish were marketable in the retail rockfish market, widow rockfish fillets began to be sold in volume with few complaints about quality.

The increased utilization of widow rockfish in 1978 was stimulated by the strong market for rockfish. A record amount of rockfish was sold, 25,000 mt, even though fishermen received a record real ex-vessel price, \$0.23/kg. Processors also received record real wholesale prices (Table 3) and fillets accounted for 80 percent of the gross revenue from rockfish (Proctor 1980).

DECLINE IN THE ROCKFISH FISHERY

Landings of most rockfish continued to increase in 1979 and 1980, but prices paid to fishermen and processors declined. I believe the price declined because the supply of rockfish exceeded the demand at the 1978 prices, and lower prices were needed to stimulate the sales of rockfish fillets. Lower prices were first reported for frozen rockfish fillets from October 1978 to March 1979. Processors realized that ex-vessel prices would also have to be lowered to enable them to sell increased supplies. Midwater trawl fishermen believed they could make a profit at a lower ex-vessel price, because they would catch large volumes of widow rockfish and maintain their gross revenues without increasing their costs.

By the winter of 1979-80, the wholesale price for fresh fillets had fallen 50 percent from the summer of 1979, and processors imposed trip limits for rockfish, Dover sole, and other species (Anonymous 1980). By the summer of 1980, the real wholesale price in Los Angeles for rockfish fillets was \$0.54/kg, compared

Table 3—Estimated sales of rockfish and Pacific ocean perch (POP)¹ by West Coast processors in 1978.

Product form	Category	Quantity (kg)	Price (\$/kg)	Real price (1967) (\$/kg)	Round weight (kg)	Conversion ² factors (%)	Processors' 1978 gross revenue (\$)
Fresh whole fish	Rockfish	1,849,633	0.74	0.37	1,849,633	0	1,368,728
	POP	139,835	1.01	0.50	139,835	0	141,233
Fresh fillets	Rockfish	4,835,973	2.62	1.31	17,271,332	28	12,670,249
	POP	1,631,446	2.82	1.41	6,525,784	25	4,600,678
Frozen fillets	Rockfish	224,469	2.82	1.41	801,675	28	502,810
	POP	129,213	2.71	1.36	516,852	25	350,167
Unspecified product	Rockfish	336,044	5.00 ³	2.50	1,680,220	20	1,680,220
	POP	31,768	2.60	1.30	127,072	25	82,596
Total		9,178,381			28,912,403		21,396,681
Actual Commercial Landing					27,557,500 ⁴		

Source: Proctor (1980). West Coast summaries of common product forms for Dungeness crab, pink shrimp and West Coast groundfish. Pacific Fishery Management Council, Portland, OR.

¹POP is separated here because of price difference with other rockfish.

²Estimated by author after discussion with processors.

³Possibly individually-wrapped portions

⁴Anonymous 1980

with the 1978 high of \$1.63/kg. In the fall of 1980 the wholesale price for rockfish fillets stabilized at about \$0.77/kg. Processors, however, could not make a profit at this price while paying fishermen at the contracted ex-vessel price of \$0.18/kg. The inability of processors to make a profit is because of the costs associated with factoring fillets. The fillet factoring costs are presented in Table 4 as a general guide to show how ex-vessel prices may affect the processors' selling price.

In 1980 the contracted real ex-vessel price for trawl-caught rockfish was \$0.18/kg. Processors needed either to restrict supply and sell at higher wholesale prices, or lower the ex-vessel price. Although some processors restricted landings of rockfish, most lowered the ex-vessel price and by October 1980 the real ex-vessel price for widow rockfish ranged from \$0.08 to \$0.13/kg. Some Oregon buyers were reported to have paid \$0.06/kg, and rumors were everywhere about still lower ex-vessel prices.

One factor contributing to the decline in ex-vessel price was that processors stopped freezing rockfish. Processors sold most rockfish fresh, because wholesale prices for frozen fillets were close to fresh fillet prices, and freezing and inventory costs added substantially to their total processing costs. Inventory costs were high because the prime interest rate was 20 percent.

Another factor thought to have contributed to the lower rockfish price is the higher risk associated with freezing and defrosting widow rockfish fillets. Whereas retailers can successfully freeze surpluses of other types of rockfish, widow rockfish fillets tend to lose quality when defrosted. Hence, retailers consider surpluses of fresh widow rockfish to be a total loss. The poor quality of defrosted widow rockfish fillets could be detrimental to the entire rockfish market if widow rockfish are not specifically labeled as such.

By December 1980, a market equilibrium appeared to exist for widow rockfish among fishermen, processors, wholesalers, and retailers at the real ex-vessel price of \$0.13/kg. This ex-vessel price is only one factor in the market equilibrium for widow rockfish fillets. Another important factor is the widow rockfish fillet yield, which is reported to be greater than or equal to other rockfish fillet yields. This yield is between 26 and 34 percent. Therefore, the raw material cost of producing widow rockfish fillets is generally less than that for producing an equal weight of other rockfish fillets.

Table 4—Comparisons of the estimated costs of producing one kilogram of rockfish fillets at five ex-vessel prices, two product yields, and a fixed 15 percent cost for profit and overhead.

Product	Yield (%)	Ex-vessel price (¢/kg)									
		6		10		12		15		20	
a) Raw material cost (¢/kg)		26	34	26	34	26	34	26	34	26	34
b) Filleting costs (¢/kg)		23	18	38	29	46	35	58	44	77	59
c) Packing costs (¢/kg)		13	13	13	13	13	13	13	13	13	13
d) 15% of a,b,c, for overhead (¢/kg)		37	37	37	37	37	37	37	37	37	37
Total cost/fillet (¢/kg)		11	10	13	12	14	13	16	14	19	16
Profit margin of 15% (¢/kg)		84	80	101	93	110	98	124	108	146	125
Processor selling price (¢/kg)		13	12	15	14	17	15	19	16	22	19
Processor selling price (¢/kg)		97	92	116	107	127	113	143	124	168	144

FUTURE OF THE WIDOW ROCKFISH FISHERY

I have presented some data from 1962 to 1980; now I will make some estimates of the widow rockfish fishery in the future. I believe that widow rockfish landings of 25,000 mt are likely by 1983. This estimate is based on the continued growth of the fishery and market, and is contingent on the size of the widow rockfish stocks, fish age-class structure within the stocks, and stock availability which allows fishermen the opportunity to catch them. Also, in the future new freezing techniques may allow widow rockfish fillets to be IQF (individually quick frozen), shattered, or made into blocks. If the ability to freeze large landings of widows can be coupled with machine filleting and packing, widow rockfish could become competitive with similar frozen products. Already, one processor in

California and one in Washington have been selling frozen widow rockfish fillets and report no complaints.

The increases in landings predicted above may not be reached unless industry guards against the marketing of even a limited amount of poor quality widow rockfish fillets. Small amounts of poor quality widow rockfish fillets could affect the entire rockfish market. If industry does not differentiate widow rockfish from other rockfish, jobbers, brokers, and retailers will have no way of knowing the shelf life of the rockfish product they buy, or if the product can be frozen. A retailer buying widow rockfish fillets under the label rockfish, rock cod, red snapper, Pacific red snapper, or Pacific snapper may freeze them unknowingly and end up with an inferior and possibly unsalable product when the fish is defrosted. Many industry persons also feel widow rockfish should be differentiated, and some do sell fillets at prices lower than other rockfish fillets. This price difference will reflect the lower ex-vessel price, higher yield of fillets, and the increased risk the retailer may be taking because of not being able to freeze surplus.

Other conditions which may retard the development of the widow rockfish fishery are:

1. Greater profitability in other fisheries.
2. Government restrictions.
3. Labor resistance to automation.
4. Social pressure within the fishing community which discourages widow rockfish fishing.

Even with all these possible negative factors, widow rockfish is sure to be the major species caught and processed by the West Coast groundfish industry in the near future, and widow rockfish products will be of good quality and relatively inexpensive to the consumer.

CITATIONS

ANONYMOUS.

1980. Pacific coast groundfish plan. Pacific Fishery Management Council, 526 Mill St., Portland, OR.

1982. Pacific coast groundfish plan. Pacific Fishery Management Council, 526 Mill Street, Portland, OR.

FISHER, R. B.

1972. An effective combination trawl for West Coast draggers: Atlantic-Western trawl. *Oreg. State Univ. Bull.* 617:1-24.

PEREYRA, W. T., and J. RICHARDS.

1970. Economic aspects of the 1967 offshore Pacific hake fishery. *U.S. Fish Wildl. Serv., Circ.* 332:103-119.

PROCTOR, R.

1980. 1978 West Coast summaries of common product forms for Dungeness crab, pink shrimp and West Coast groundfishes. Pacific Fishery Management Council, 526 Mill St., Portland, OR.

SCOFIELD, W. L.

1948. Trawling gear in California. *Calif. Dep. Fish Game, Fish Bull.* 72:1-60.

POSTSCRIPT

Landings of widow rockfish have exceeded my prediction of 25,000 mt per year as early as 1981, when 28,000 mt were landed. In 1982, 26,000 mt is estimated to have been landed. These large catches of widow rockfish exceed the maximum sustainable yield of the widow rockfish stocks (Anonymous 1982). In 1983 a total allowable catch of 10,500 mt and a trip limit have been established. The real ex-vessel price of widow rockfish for 1983 is contracted at \$0.15/kg, which is roughly its mode price over the last 20 years. With these restrictions, many of the fishermen who relied on widow rockfish will have to fish for other groundfish off California, Oregon, Washington, and Alaska.

Composition of the Incidental Kill of Small Cetaceans in the US Purse-Seine Fishery for Tuna in the Eastern Tropical Pacific during 1985

Bruce E. Wahlen, Ruth B. Miller, and Carolyn J. Macky

Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, California 92038, USA

ABSTRACT

Composition of incidental kill of small cetaceans by US registered purse-seiners fishing in the eastern tropical Pacific during 1985 is reported by area, species, stock, sex, length and reproductive condition. The data were collected by technicians of the Inter-American Tropical Tuna Commission and of the National Marine Fisheries Service during 53 vessel-trips.

INTRODUCTION

Several papers describing small cetacean kill incidental to fishing activities of tuna purse-seiners in the eastern tropical Pacific (ETP) have been published, as noted by Wahlen, Walker, Miller and Oliver (1986) and by Hall and Boyer (1986; 1987). In this fourth in a series of papers (Perrin and Oliver, 1982; Oliver, Walker and Miller, 1983; Wahlen, *et al.*, 1986), we report the incidental kill of small cetaceans by US registered vessels in the ETP during 1985. These kills are classified by area, species, stock, sex, length and reproductive condition. Species represented in this report are: pantropical spotted dolphins, *Stenella attenuata*; spinner dolphins, *S. longirostris*; striped dolphins, *S. coeruleoalba*; common dolphins, *Delphinus delphis*; rough-toothed dolphins, *Steno bredanensis*; and bottlenose dolphins, *Tursiops truncatus*.

DATA AND METHODS

Data were collected by Inter-American Tropical Tuna Commission (IATTC) and National Marine Fisheries Service (NMFS) technician-observers aboard a sample of US registered tuna purse-seine vessels fishing in the ETP (Lo, Powers and Wahlen, 1982). Data collected aboard US registered tuna seiners chartered by non-US companies were also included.

Observed kills by area, species, stock and sex, if determined, were obtained from the 'tally' databases. Length frequencies by sex and reproductive condition for females were obtained from the 'life history' databases containing extensive biological data for those dead animals which were available for 'hands-on' inspection by the technicians. The life history databases thus contain biological data for only a subset of the animals reported as killed in the tally databases, since the technicians are unable to physically examine each animal killed. See Perrin and Oliver (1982) for detailed descriptions of data recorded in these databases.

We allocated kills of offshore spotted and whitebelly spinner dolphins to geographic stocks as in Perrin and Oliver (1982). Laboratory procedures for processing specimens and determining sexual maturity are referenced in Perrin and Oliver (1982), as is the methodology of the computer programs used to summarize the reproductive condition data.

RESULTS AND DISCUSSION

Kill data were collected from each of 53 observed trips, including five trips by US seiners chartered by non-US companies. The geographical distribution of the kill is presented in Fig. 1. Kill data are summarized by stock, sex and area for 5,484 spotted dolphins (Table 1) and 2,863 spinner dolphins (Table 2); by sex and area for 431 common, 23 striped, 1 rough-toothed and 37 bottlenose dolphins (Table 3); and by area only for 157 unidentified dolphins (Table 3). In Tables 1-3, which were obtained from the tally databases, the stock or species totals may be larger than the sum over sexes because the sex of some animals in the tally databases was not determined. The unidentified dolphins (Table 3) were likely spotted or spinner dolphins which were not seen closely enough for identification.

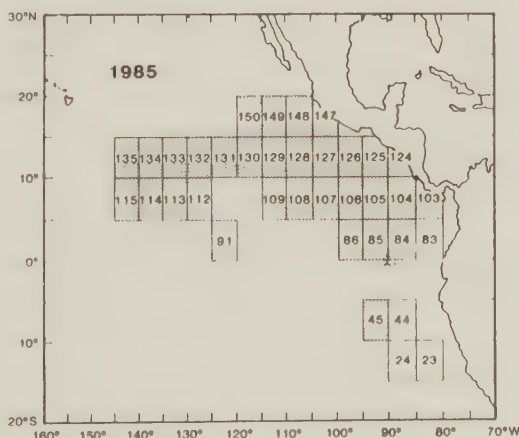


Fig. 1. Five-degree blocks in the eastern tropical Pacific Ocean in which dolphins were killed during fishing operations of US vessels in 1985. Numbered blocks without shading indicate areas in which tally data only were collected. Numbered blocks with shading indicate areas in which both tally and life history data were collected. Blocks without a number indicate areas in which no dolphin kills were recorded.

Length frequencies for sexed animals are tabulated by stock for 1,495 spotted and 586 spinner dolphins (Table 4) and by species for 176 common, 1 striped, 1 rough-toothed

and 14 bottlenose dolphins (Table 5). The length frequency totals (Tables 4 and 5) are less than or equal to the kill by sex and area totals (Tables 1-3) because lengths were obtained from the life history databases, which contain data for only a subset of the animals in the tally databases. Female reproductive condition results are reported by stock for 810 spotted and 294 spinner dolphins (Table 6) and by species for 83 common and 6 striped dolphins (Table 7).

Table 1

Total kill of spotted dolphins by observed US vessels during 1985, by stock, sex (M = male, F = female), and 5 degree block. No kills were reported for the coastal stock.

5° block	Northern offshore			Southern offshore			5° block	Northern offshore			Southern offshore		
	M	F	Total	M	F	Total		M	F	Total	M	F	Total
23	0	0	0	1	4	16	115	0	1	2	0	0	0
24	0	0	0	3	7	24	124	5	4	96	0	0	0
44	0	0	0	3	1	19	125	167	180	767	0	0	0
83	1	3	10	0	0	0	126	23	26	86	0	0	0
84	4	8	46	0	0	0	127	8	11	166	0	0	0
85	7	5	61	0	0	0	128	42	49	443	0	0	0
86	7	3	21	0	0	0	129	0	4	13	0	0	0
91	15	6	21	0	0	0	130	2	2	94	0	0	0
103	2	1	3	0	0	0	131	6	9	78	0	0	0
104	26	34	140	0	0	0	132	72	91	235	0	0	0
105	74	74	847	0	0	0	133	23	29	71	0	0	0
106	110	126	590	0	0	0	134	18	12	105	0	0	0
107	64	95	702	0	0	0	135	2	2	9	0	0	0
108	30	44	300	0	0	0	147	0	3	7	0	0	0
109	1	1	2	0	0	0	148	4	6	15	0	0	0
112	14	13	35	0	0	0	149	38	37	117	0	0	0
113	49	55	173	0	0	0	150	2	7	97	0	0	0
114	9	15	73	0	0	0	Total	825	956	5,425	7	12	59

Table 2

Total kill of spinner dolphins by observed US vessels during 1985, by stock, sex (M = male, F = female), and 5 degree block number. Reported kill of 65 unidentified spinner dolphins is not included. No kills were reported for the Costa Rican stock.

5° block	Eastern			Northern whitebelly			Southern whitebelly		
	M	F	Total	M	F	Total	M	F	Total
24	0	0	0	0	0	0	76	79	267
44	9	5	18	0	0	0	0	0	237
45	0	0	0	0	0	0	1	0	2
84	0	1	2	0	2	3	0	0	0
85	1	3	7	4	4	33	0	0	0
86	0	0	0	2	2	11	0	0	0
103	0	0	0	0	1	1	0	0	0
104	0	0	0	0	4	4	0	0	0
105	0	0	1	4	8	58	0	0	0
106	8	9	18	14	19	58	0	0	0
107	10	10	86	17	11	122	0	0	0
108	8	4	64	4	5	25	0	0	0
109	1	0	1	0	0	0	0	0	0
112	0	0	0	4	5	16	0	0	0
113	0	0	0	19	30	72	0	0	0
114	0	0	0	3	11	190	0	0	0
115	0	0	0	10	3	14	0	0	0
124	0	0	1	0	0	0	0	0	0
125	108	102	321	0	0	1	0	0	0
126	22	27	135	2	1	3	0	0	0
127	8	6	41	0	1	2	0	0	0
128	44	38	401	0	0	1	0	0	0
129	0	0	10	0	0	0	0	0	0
130	7	8	24	0	0	0	0	0	0
131	4	1	22	3	2	6	0	0	0
132	1	2	5	21	18	81	0	0	0
133	0	0	0	12	8	29	0	0	0
134	0	0	0	19	21	195	0	0	0
135	0	0	0	23	25	177	0	0	0
147	0	1	1	0	0	0	0	0	0
148	0	1	3	0	0	0	0	0	0
149	2	3	15	0	0	0	0	0	0
150	1	1	79	0	0	0	0	0	0
Total	234	222	1,255	161	181	1,102	77	79	506

Table 3

Total kill of common, striped, rough-toothed and bottlenose dolphins by observed US vessels during 1985, by sex (M = male, F = female) and 5 degree block number. Total kills only are included for unidentified dolphins since sex was not determined for these animals. T = total. Unid. = unidentified.

5° block	Common			Striped			Rough-toothed			Bottlenose			Unid.
	M	F	T	M	F	T	M	F	T	M	F	T	
103	2	1	3	0	0	0	0	0	0	0	0	0	0
104	10	15	34	0	0	0	0	0	0	0	0	0	0
105	60	56	310	0	0	0	0	0	0	0	0	1	0
106	8	11	28	0	0	0	0	0	0	3	0	3	0
107	0	0	0	0	0	0	0	0	0	0	0	2	124
108	0	0	0	0	0	0	1	0	1	0	0	0	2
112	0	0	0	0	0	0	0	0	0	2	0	2	0
113	0	0	0	0	0	0	0	0	0	0	0	0	10
124	13	8	34	0	0	0	0	0	0	0	0	0	0
125	14	8	22	0	0	0	0	0	0	3	8	21	16
126	0	0	0	0	0	0	0	0	0	2	0	3	0
127	0	0	0	0	0	0	0	0	0	1	0	1	0
128	0	0	0	0	0	0	0	0	0	0	0	4	2
131	0	0	0	1	0	23	0	0	0	0	0	0	1
133	0	0	0	0	0	0	0	0	0	0	0	0	2
Total	107	99	431	1	0	23	1	0	1	11	8	37	157

Table 4

Length frequencies of northern offshore spotted dolphins and of eastern and northern whitebelly spinner dolphins killed by observed US vessels during 1985, by sex (M = male, F = female). Reported kills of one male southern offshore spotted dolphin in each of three length categories (160-164 cm, 175-179 cm, 195-199 cm) and of 22 unidentified spinner dolphins are not included. No kills were reported for coastal spotted, Costa Rican spinner, or southern whitebelly spinner dolphins.

Length (cm)	Northern offshore		Eastern		Northern whitebelly	
	M	F	M	F	M	F
0-59	0	0	0	0	0	0
60-64	0	1	0	0	0	0
65-69	0	0	0	0	0	0
70-74	0	0	0	0	0	0
75-79	0	2	1	0	0	0
80-84	2	0	0	0	0	1
85-89	5	5	1	0	0	0
90-94	2	3	0	0	2	1
95-99	4	8	1	0	1	0
100-104	7	8	0	1	5	3
105-109	5	6	2	1	0	2
110-114	4	6	1	3	3	2
115-119	8	6	0	2	0	0
120-124	7	5	1	4	1	1
125-129	7	11	3	5	1	0
130-134	8	9	1	1	0	1
135-139	16	7	4	2	3	3
140-144	10	10	1	2	4	5
145-149	14	20	5	11	4	5
150-154	15	15	6	7	4	10
155-159	33	23	23	16	2	10
160-164	46	38	13	20	17	6
165-169	64	57	34	31	10	17
170-174	75	67	33	28	12	25
175-179	84	78	20	13	16	19
180-184	49	94	18	13	19	13
185-189	49	103	7	1	7	7
190-194	44	131	1	0	6	1
195-199	37	58	0	0	0	0
200-204	34	26	0	0	0	0
205-209	23	10	0	0	0	0
210-214	20	3	0	0	0	0
215-219	8	0	0	0	0	0
220-224	1	0	0	0	0	0
225-229	1	0	0	0	0	0
230-	0	0	0	0	0	0
Total	682	810	176	161	117	132

Perrin, Scott, Walker and Cass (1985) reviewed all body length data for specimens collected through 1981. Some of the male northern offshore spotted dolphin specimens were quite large (Table 4); however, all lengths were

within the range of body lengths observed by Perrin *et al.* (1985). The female northern offshore spotted dolphin in the 60-64 cm length category (Table 4) may have been an aborted fetus.

Finally, it should be noted that Hohn and Scott (1983) have identified a sampling bias in the life history data resulting from the collection process. The magnitude of the effect of this bias on the life history statistics presented here (Tables 4-7) is unknown but will probably not significantly affect life history parameter estimates (A. Hohn, Southwest Fisheries Center, P.O. Box 271, La Jolla, California, 92038, USA, pers. comm., May 1986).

Table 5

Length frequencies of common and bottlenose dolphins killed by observed US vessels during 1985, by sex (M = male, F = female). Reported kills of one male striped dolphin (210-214 cm) and one male rough-toothed dolphin (170-174 cm) are not included.

Length (cm)	Common		Bottlenose		Length (cm)	Common		Bottlenose	
	M	F	M	F		M	F	M	F
0-89	0	0	0	0	190-194	11	14	1	0
90-94	0	2	0	0	195-199	11	11	0	0
95-99	1	0	0	0	200-204	10	15	0	0
100-104	1	3	0	0	205-209	11	6	0	1
105-109	4	0	0	0	210-214	12	1	1	0
110-114	1	3	0	0	215-219	8	0	0	0
115-119	0	1	0	0	220-224	4	0	1	0
120-124	1	0	0	0	225-229	0	0	0	0
125-129	1	1	0	0	230-234	0	0	1	0
130-134	1	1	0	0	235-239	0	0	2	0
135-139	1	0	0	0	240-244	0	0	0	2
140-144	0	0	0	0	245-249	0	0	0	1
145-149	1	0	0	0	250-254	0	0	0	1
150-154	2	0	0	0	255-259	0	0	1	0
155-159	2	1	0	0	260-264	0	0	1	0
160-164	1	4	0	0	265-269	0	0	0	0
165-169	0	0	0	0	270-274	0	0	0	0
170-174	3	3	0	0	275-279	0	0	1	0
175-179	3	5	0	0	280-	0	0	0	0
180-184	1	4	0	0					
185-189	4	6	0	0	Total	95	81	9	5

Table 6

Reproductive condition of female northern offshore spotted dolphins and of female eastern and northern whitebelly spinner dolphins killed by observed US vessels during 1985. Both sample sizes (N) and percentages (%) are indicated. Reproductive condition information was not obtained for coastal spotted, southern offshore spotted, Costa Rican spinner or southern whitebelly spinner dolphins. U = Maturity undetermined; I = Sexually immature; MU = Sexually mature, lactation undetermined; P = Pregnant only; PL = Pregnant and lactating; L = Lactating only; RCL = 'Resting' with corpus luteum; R = 'Resting' without corpus luteum; PR = Post-reproductive.

Reproductive condition	Northern offshore		Eastern		Northern whitebelly	
	N	%	N	%	N	%
U	472	58.3	103	63.6	63	47.7
I	150	18.5	40	24.7	37	28.0
MU	5	0.6	1	0.6	1	0.8
P	43	5.3	5	3.1	2	1.5
PL	12	1.5	1	0.6	1	0.8
L	87	10.7	7	4.3	15	11.4
RCL	3	0.4	0	0.0	2	1.5
R	37	4.6	4	2.5	10	7.6
PR	1	0.1	1	0.6	1	0.8
Total	810	100.0	162	100.0	132	100.0

Table 7

Reproductive condition of female common and bottlenose dolphins killed by observed US vessels during 1985. Both sample sizes (N) and percentages (%) are indicated. Reproductive condition information for striped and rough-toothed dolphins is not included; none were females. Abbreviations are as in Table 6.

Reproduct. condition	Common		Bottlenose		Reproduct. condition	Common		Bottlenose	
	N	%	N	%		N	%	N	%
U	47	56.6	2	33.3	L	9	10.8	3	50.0
I	16	19.3	0	0.0	RCL	0	0.0	0	0.0
MU	1	1.2	0	0.0	R	1	1.2	0	0.0
P	7	8.4	1	16.7	PR	0	0.0	0	0.0
PL	2	2.4	0	0.0	Total	83	100.0	6	100.0

ACKNOWLEDGEMENTS

We wish to thank the staff of the Inter-American Tropical Tuna Commission and the staff of the NMFS, both at the Southwest Region and at the Southwest Fisheries Center, for providing data for this report. In addition, we acknowledge the assistance of H. Bernard in processing the specimens, H. Orr in drafting the figure, and M. Ragan and C. Ratcliffe in typing the manuscript. We also thank M. Hall, Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, California, 92093, USA, and W. Perrin, Southwest Fisheries Center, P.O. Box 271, La Jolla, California, 92038, USA, for critical review of this manuscript.

REFERENCES

- Hall, M.A. and Boyer, S.D. 1986. Incidental mortality of dolphins in the eastern tropical Pacific tuna fishery: description of a new method and estimation of 1984 mortality. *Rep. int. Whal. Commn* 36: 375-81.
- Hall, M.A. and Boyer, S.D. 1987. Incidental mortality of dolphins in the eastern tropical Pacific tuna fishery in 1985. Paper SC/38/SM5 (published in this volume).
- Hohn, A.A. and Scott, M.D. 1983. Segregation by age in schools of spotted dolphins in the eastern tropical Pacific. Abstract, Fifth Biennial Conference on the Biology of Marine Mammals, Boston, USA.
- Lo, N.C.H., Powers, J.E. and Wahlen, B.E. 1982. Estimating and monitoring incidental dolphin mortality in the eastern tropical Pacific tuna purse seine fishery. *Fish. Bull.*, U.S. 80(2): 396-401.
- Oliver, C.W., Walker, G.J. and Miller, R.B. 1983. Time/area distribution and composition of the incidental kill of small cetaceans in the U.S. purse-seine fishery for tuna in the eastern tropical Pacific during 1981. *Rep. int. Whal. Commn* 33: 603-15.
- Perrin, W.F. and Oliver, C.W. 1982. Time/area distribution and composition of the incidental kill of dolphins and small whales in the U.S. purse-seine fishery for tuna in the eastern tropical Pacific, 1979-80. *Rep. int. Whal. Commn* 32: 429-44.
- Perrin, W.F., Scott, M.D., Walker, G.J. and Cass, V.L. 1985. Review of geographical stocks of tropical dolphins (*Stenella* spp. and *Delphinus delphis*) in the eastern Pacific. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 28, 28 pp.
- Wahlen, B.E., Walker, G.J., Miller, R.B. and Oliver, C.W. 1986. Composition of the incidental kill of small cetaceans in the US purse-seine fishery for tuna in the eastern tropical Pacific, 1982 through 1984. *Rep. int. Whal. Commn* 36: 369-74.

Estimating Growth and Mortality in Steady-State Fish Stocks from Length-Frequency Data

J.A. WETHERALL

J.J. POLOVINA

S. RALSTON

Southwest Fisheries Center, Honolulu Laboratory

National Marine Fisheries Service, NOAA

2570 Dole St., Honolulu, Hawaii 96822-2396

USA

Wetherall, J.A., J.J. Polovina and S. Ralston. 1987. Estimating growth and mortality in steady-state fish stocks from length-frequency data, p. 53-74. *In* D. Pauly and G.R. Morgan (eds.) *Length-based methods in fisheries research*. ICLARM Conference Proceedings 13, 468 p. International Center for Living Aquatic Resources Management, Manila, Philippines, and Kuwait Institute for Scientific Research, Safat, Kuwait.

Abstract

Methods of using length-frequency statistics to estimate L_{∞} and the ratio Z/K in steady-state fish stocks with von Bertalanffy growth and exponential mortality are studied. Several standard procedures applicable when mortality is constant are reviewed, and new methods are introduced which have superior performance. The various methods are evaluated using Monte Carlo techniques. Problems of systematic bias are discussed, and remedial measures are suggested. Finally, a method is developed (but not yet evaluated) to estimate length-specific mortality rates under the steady-state model.

Introduction

The current revival of interest in length-frequency based stock assessment methods has led to several new techniques which provide fisheries biologists with alternatives to well-established procedures or allow analysis in situations where traditional age-based methods are infeasible. Because age estimation is often difficult and usually expensive, length-frequency based methods may be the most efficient and reliable means for estimating some of the key parameters of fishery models (see Mathews, Part I, this vol.).

Most of the new length-based procedures, like the graphical and manual methods they are designed to replace, are applicable to situations where spawning is periodic and the identity of cohorts is adequately maintained in the population's length-frequency distribution. Under such circumstances, it is possible to estimate jointly parameters of growth, mortality and recruitment by fitting composite models to single length-frequency samples (e.g., Schnute and Fournier 1980), or to sequences of samples taken over time (e.g., Pauly and David 1981). Estimation and hypothesis testing are facilitated by adopting specific structural assumptions on the underlying processes and

then maximizing likelihood functions or fitting model expectations to observed length class frequencies by least squares or other criteria. Solutions are found by iterative search techniques which take advantage of, and indeed require, the numerical power of computers.

Less attention has been paid lately to the relatively simple methods applicable in situations where cohorts are not clearly distinguishable in catch length distributions, individual length-frequency samples are too small to be treated separately, first approximations are adequate, or sophisticated computer systems and optimization software are unavailable. Among these simple methods, probably the best known is the formula due to Beverton and Holt (1956):

$$Z = K \left(\frac{L_{\infty} - \bar{\ell}}{\bar{\ell} - L_c} \right) \quad \dots 1)$$

which estimates the total instantaneous mortality coefficient, Z , in a steady-state population with constant exponential mortality and von Bertalanffy growth, from the mean length, $\bar{\ell}$, in a random sample of fish above length L_c . In using (1), it is assumed that L_c and the von Bertalanffy parameters, K and L_{∞} , are given. If only L_c and L_{∞} are known (or estimated from other information), slight rearrangement of (1) yields an estimate of the ratio $\theta = Z/K$, a component of many standard yield models and stock assessment procedures (see Gulland 1983).

The Beverton-Holt formula represents a particular class of methods for computing analytical estimates of growth and mortality parameters on the basis of length-frequency data, procedures requiring rather strong assumptions but whose use is justified by their simplicity and their robustness under variable recruitment. This paper reviews three such methods reported in the literature, and introduces some new ones which require more computation but the same amount, or less, input information. First, the assumptions underlying the steady-state methods are given and a structure for length-frequency samples is described. Next, estimators based on the assumption of constant mortality rate are discussed, followed by a consideration of systematic biases. Next, the assumption of constant mortality is relaxed and methods for estimating length-specific mortality are developed. Finally, some Monte Carlo experiments on the constant-mortality methods are described; the concluding section offers advice on use of the various procedures.

Basic Assumptions

PROBABILITY DENSITY OF FISH LENGTHS

In all the methods treated here, a steady-state population is assumed. Growth is assumed to follow the deterministic von Bertalanffy curve with parameters K and L_{∞} . The curve's location parameter, t_0 , usually included in modelling length at age, is omitted since it does not influence length-frequency distributions. Unless otherwise stated, mortality of fish above a knife-edge selection size, L_c , is assumed to occur at a constant instantaneous rate, Z , and recruitment to this size to take place at a constant instantaneous rate, R .

Under these conditions, the probability density ($g(\ell)$) of fish length in the sampled stock is

$$g(\ell) = \frac{\theta (L_{\infty} - \ell)^{\theta - 1}}{(L_{\infty} - L_c)^{\theta}} \quad L_c \leq \ell < L_{\infty} \quad \dots 2)$$

On integrating (2), the cumulative length-distribution function ($G(\ell)$) is seen to be

$$G(\ell) = 1 - \left(\frac{L_\infty - \ell}{L_\infty - L_c} \right)^\theta \quad \dots 3)$$

$$L_c \leq \ell < L_\infty$$

and the mean and variance of length for fish above length L_c are

$$E(\ell) = L_\infty - \left(\frac{\theta}{\theta + 1} \right) (L_\infty - L_c) \quad \dots 4)$$

and

$$V(\ell) = \left(\frac{\theta}{\theta + 2} \right) \left(\frac{L_\infty - L_c}{\theta + 1} \right)^2 \quad \dots 5)$$

A convenient ancillary variable may be defined as $X = \ell/L_\infty$, the actual length of a fish in proportion to its maximum possible length. By changing variables in (2) it is seen that the density for X is

$$h(X) = \frac{\theta (1 - X)^{\theta - 1}}{(1 - X_c)^\theta} \quad \dots 6)$$

$$X_c \leq X < 1$$

where $X_c = L_c/L_\infty$, and its distribution function is

$$H(X) = 1 - \left(\frac{1 - X}{1 - X_c} \right)^\theta \quad \dots 7)$$

SAMPLING SCHEME

It is assumed that a random sample of n fish is taken from $g(\ell)$ above the minimum catchable size, L_c , with lengths $\ell_1, \ell_2, \dots, \ell_n$. We assume the lengths are observed without error. In practice this assumption is usually violated, but the consequences may not be serious unless measurement errors are very large. We also assume, more critically, that there is no systematic measurement bias.

Measurement error aside, observed fish lengths are recorded with various degrees of "accuracy." As a result, sample length-frequency distributions range from the very sparse (multiple observations of a given length being uncommon in samples of moderate size) to the highly aggregated (the data

being grouped into relatively few length intervals, each containing relatively many observations). To describe each data set we adopt a general scheme wherein the n sample observations are grouped into $r > 2$ contiguous length intervals, each fish in a particular interval being assigned a length equal to the interval midpoint. Let $\tilde{\ell}_i$ denote the midpoint of the i -th interval of width Δ_i ($i = 1, 2, \dots, r$). We define $L_{\min}$ as the lower bound of the first length interval and $L_{\max}$ as the upper bound of the last interval, i.e., $L_{\min} = \tilde{\ell}_1 - \Delta_1/2$, and $L_{\max} = \tilde{\ell}_r + \Delta_r/2$. A data set consists of a set of length interval midpoints $\{\tilde{\ell}_1, \tilde{\ell}_2, \dots, \tilde{\ell}_r\}$ and a corresponding set of frequencies $\{n_1, n_2, \dots, n_r\}$. (Note that the interval frequencies sum to the total sample size, n .)

Estimators

The procedures used to estimate growth and mortality parameters from length-frequency samples differ in their statistical properties, the assumptions they require, and the amount of information they produce. In this section, assuming constant mortality, we review three established methods and explore several new approaches. We first examine some methods applicable when both L_c and L_∞ are known and only θ is to be estimated. Then we consider the joint estimation of θ and L_∞ when only L_c is given.

BEVERTON-HOLT METHOD

The classical formula for $\hat{\theta}$, given by rearranging (1), is

$$\hat{\theta}_{BH} = \frac{L_\infty - \bar{\ell}}{\bar{\ell} - L_c} \quad \dots 8)$$

It was derived in a non-probabilistic way by Beverton and Holt (1956), from an expression for mean length in the catch. However, it is readily seen that $\hat{\theta}_{BH}$ is identical to the moment estimator based formally on the density at (2) and the resulting expected length (4). Further analysis with Taylor series shows that $\hat{\theta}_{BH}$ has a statistical bias approximately equal to

$$\text{Bias}(\hat{\theta}_{BH}) = \frac{\theta(\theta + 1)}{n(\theta + 2)} \quad \dots 9)$$

and a large-sample variance of

$$\text{Var}(\hat{\theta}_{BH}) = \frac{\theta(\theta + 1)^2}{n(\theta + 2)} \quad \dots 10)$$

In constructing $\hat{\theta}_{BH}$, L_∞ and L_c were assumed known. However, this is never true, so in applying $\hat{\theta}_{BH}$ independent estimates of these parameters, or simply educated guesses, must be substituted. The statistical properties of $\hat{\theta}_{BH}$ are consequently altered, so that (9) and (10) no longer apply. This problem of systematic bias will be discussed in a later section.

SSENTONGO-LARKIN METHOD

Ssentongo and Larkin (1973) also assumed L_c and L_∞ were known. They developed an estimator for θ by first deriving a moment estimator for Z , based on the mean age of fish in the sample, and then, given the assumed relationship between length and age, changing variables. The resulting expression, assuming fish lengths are measured and recorded exactly, is

$$\hat{\theta}_{SL} = (\bar{y} - y_c)^{-1} \quad \dots 11)$$

where

$$\bar{y} = -\frac{1}{n_i} \sum_{i=1}^{n_i} \ln \left(1 - \frac{\ell_i}{L_\infty} \right) = -\frac{1}{n_i} \sum_{i=1}^{n_i} \ln (1 - X_i)$$

and

$$y_c = -\ln (1 - X_c)$$

It may readily be shown that $\hat{\theta}_{SL}$ is also the maximum likelihood estimator based on the density at (6), and is a special case of a more general maximum likelihood procedure discussed later.

As Ssentongo and Larkin report, $\hat{\theta}_{SL}$ has a statistical bias of

$$\text{Bias}(\hat{\theta}_{SL}) = \frac{\theta}{n_i} \quad \dots 12)$$

and a large-sample variance of

$$\text{Var}(\hat{\theta}_{SL}) = \frac{\theta^2}{n_i} \quad \dots 13)$$

Thus the bias of $\hat{\theta}_{SL}$ is greater than that of $\hat{\theta}_{BH}$, but its asymptotic variance is smaller, as expected.

As in the Beverton-Holt estimator, the properties of $\hat{\theta}_{SL}$ are altered in practice, since L_∞ and L_c must invariably be estimated. Note further that the estimate of L_∞ must exceed $L_{\max}$; we return to this point later.

POWELL METHOD

Powell (1979) considered the problem of estimating both θ and L_∞ in a more general context, in which the asymptotic lengths of fish in a population are regarded as random variables, λ , with expectation L_∞ and variance σ_λ^2 . Of various estimation schemes suggested by Powell, the most

interesting is based on use of the first and second moments of the resulting probability distribution of ℓ . Manipulation of Powell's results (Equations (4) and (6) in his paper) reveals that

$$E(\ell) = L_{\infty} - \left(\frac{\theta}{\theta + 1} \right) (L_{\infty} - L_c) \quad \dots 14)$$

and

$$V(\ell) = \left(\frac{1}{\theta + 2} \right) \left\{ \theta \left(\frac{L_{\infty} - L_c}{\theta + 1} \right)^2 + 2\sigma_{\lambda}^2 \right\} \quad \dots 15)$$

We suppose L_c is given. Then, provided σ_{λ}^2 is known, or the range of λ is negligible compared with the expected maximum range of ℓ in the data (in which case set $\sigma_{\lambda}^2 = 0$), $E(\ell)$ and $V(\ell)$ can be equated to the corresponding sample statistics and solved for θ and L_{∞} . Let $\bar{\ell}$ denote the sample mean length for fish above L_c , and S_{ℓ}^2 the sample variance. Then the resulting moment estimators of θ and L_{∞} (when $\sigma_{\lambda}^2 = 0$) are

$$\hat{\theta}_P = \frac{2S_{\ell}^2}{(\bar{\ell} - L_c) - S_{\ell}^2} \quad \dots 16)$$

and

$$\begin{aligned} \hat{L}_{\infty P} &= \bar{\ell} + \frac{2S_{\ell}^2 (\bar{\ell} - L_c)}{(\bar{\ell} - L_c)^2 - S_{\ell}^2} \quad \dots 17) \\ &= \bar{\ell} + \hat{\theta}_P (\bar{\ell} - L_c) \end{aligned}$$

Since Powell's method makes use of additional information in the sample to estimate L_{∞} , $\hat{\theta}_P$ is a considerable improvement over $\hat{\theta}_{BH}$ and $\hat{\theta}_{SL}$ when accurate, independent information on L_{∞} is unavailable.

REGRESSION METHOD

Another method for estimating θ and L_{∞} jointly may be developed by considering the equation at (4), and exploiting the fact that $E(\ell)$ is a linear function of L_c . Let $\{w_1, w_2, \dots, w_m\}$ be an increasing sequence of fish lengths in the interval (L_c, L_{∞}) . For a random sample of lengths in

this interval, let $\bar{\ell}_j$ denote the average length of the n_j fish in the sample whose length exceeds w_j . It follows from (4) that

$$E(\bar{\ell}_j) = L_\infty \left(\frac{1}{1 + \theta} \right) + w_j \left(\frac{\theta}{1 + \theta} \right) \quad \dots 18)$$

$$j = 1, 2, \dots, m$$

i.e., $E(\bar{\ell}_j)$ is linear in w_j . The idea of the method is to partition the length-frequency sample using a specified sequence $\{w\}$ and estimate α and β in the linear regression model

$$\bar{\ell}_j = \alpha + \beta w_j + \varepsilon_j \quad \dots 19)$$

where the ε_j are random errors with zero mean and covariance matrix A . Minimum variance unbiased estimates of α and β are found by weighted least squares, using the weight matrix A^{-1} . An estimate of A may be computed from the sample statistics, the (i, j) -th element being

$$A_{ij} = \text{Cov}(\bar{\ell}_i, \bar{\ell}_j) = \sigma_j^2/n_i \quad \dots 20)$$

where σ_j^2 is the variance among the n_j lengths in the smaller, "included" sample, i.e., the variance among the common elements in the i -th and j -th partitions.

Consistent estimates of θ and L_∞ are then provided by

$$\hat{\theta}_R = \frac{\hat{\beta}}{1 - \hat{\beta}} \quad \dots 21)$$

and

$$\hat{L}_{\infty R} = \frac{\hat{\alpha}}{1 - \hat{\beta}} \quad \dots 22)$$

Although the choice of divisions in the length-frequency distribution is somewhat arbitrary, there is undoubtedly some optimal partitioning. To a degree, precision in parameter estimates is increased by creating more partitions (data points). One possibility is to let the observed length interval mid-points define a set of partitions, resulting in r data points for the regression, namely,

$$w_j = \tilde{\ell}_j - \frac{\Delta_j}{2} \quad \dots 23)$$

and

$$\bar{\ell}_j = \frac{\sum_{i=j}^r \tilde{\ell}_i n_i}{\sum_{i=j}^r n_i} \quad j = 1, 2, \dots, r.$$

The drawback to this approach is that a large weight matrix must be inverted. The task is greatly simplified when fewer data points are created. In particular, if the divisions are not close together the covariances among the partitions are reduced. Acceptable results can then be obtained by ignoring the off-diagonal elements of A , and weighting the mean lengths by the reciprocals of their variances, or simply by the partition sample sizes.

Asymptotic variances and covariances among the estimates of θ and L_∞ are approximately

$$\text{Var}(\hat{\theta}_R) = \frac{\sigma_{\hat{\beta}}^2}{(1-\beta)^4} \quad \dots 24)$$

$$\text{Var}(\hat{L}_{\infty R}) = \frac{1}{(1-\beta)^2} \left\{ \sigma_{\hat{\alpha}}^2 + \left(\frac{\alpha}{1-\beta} \right)^2 \sigma_{\hat{\beta}}^2 + \left(\frac{2\alpha}{1-\beta} \right) \sigma_{\hat{\alpha}, \hat{\beta}} \right\} \quad \dots 25)$$

and

$$\text{Cov}(\hat{\theta}_R, \hat{L}_{\infty R}) = \frac{\alpha}{(1-\beta)^4} \sigma_{\hat{\beta}}^2 + \frac{1}{(1-\beta)^3} \sigma_{\hat{\alpha}, \hat{\beta}} \quad \dots 26)$$

Another linear regression approach has been developed by Jones (1981). From (3), observe that the probability of a fish length exceeding w is

$$P(w) = 1 - G(w) \quad \dots 27)$$

$$= \left(\frac{L_\infty - w}{L_\infty - L_c} \right)^\theta.$$

This may be estimated empirically by $p(w)$, the proportion of fish in the sample whose length exceeds w . Jones, assuming L_c and L_∞ are known, suggests plotting $\ln P(w_i)$ vs. $\ln(L_\infty - w_i)$, $i = 1, 2, \dots, m$ and estimating θ as the slope of a regression line fit to these points. We note that if this regression is fitted by least squares, an appropriate weighting scheme should be used to account for the correlated errors in the sequence of $\ln P(w)$. There are also unresolved questions related to choice of partitions.

Some other regression methods are discussed in a later section.

MAXIMUM LIKELIHOOD METHOD

If n_i fish are sampled from the density (2), and assigned to length interval midpoints as described above, the joint likelihood of the length-frequency sample is

$$\mathcal{L} = \prod_{i=1}^r f_i^{n_i} \quad \dots 28)$$

where

$$f_i = \frac{[L_\infty - (\tilde{\ell}_i - \frac{\Delta_i}{2})]^\theta - [L_\infty - (\tilde{\ell}_i + \frac{\Delta_i}{2})]^\theta}{(L_\infty - L_c)^\theta} \quad \dots 29)$$

is the probability of falling in the i -th length class interval. When the Δ_i are small, the exact interval probabilities may be approximated by

$$f'_i = \frac{\theta (L_\infty - \tilde{\ell}_i)^{\theta-1} \Delta_i}{(L_\infty - L_c)^\theta} \quad \dots 30)$$

For any values of θ and L_∞ , $\mathcal{L}$ is maximized by setting L_c as large as possible. Therefore, under the sampling scheme adopted here, the maximum likelihood estimate of L_c is $L_{\min}$. Further, when $\theta = 1$, the maximum likelihood estimate of L_∞ is $L_{\max}$. Except in this singular case, the joint maximum likelihood estimates of θ and L_∞ ($\hat{\theta}_{ML}$ and $\hat{L}_{\infty ML}$) must be found numerically, applying iterative search methods to $\mathcal{L}$ or $\ln \mathcal{L}$. If Newton-type methods are used, the asymptotic covariance matrix for the estimates is also easily computed. Note that in the search for $\hat{L}_{\infty ML}$, $L_{\max}$ is a lower bound. Observe also that if both L_c and L_∞ are assumed known, the maximum likelihood estimator of θ is identical to the Ssentongo-Larkin estimator, $\hat{\theta}_{SL}$.

Another likelihood model may be constructed by considering the conditional probabilities of the length class frequencies given the total sample. Such frequencies are multinomial with probabilities

$$\mu_i = f_i / \sum_{i=1}^r f_i \quad \dots 31)$$

From (29), we have

$$\mu_i = \frac{[L_\infty - (\tilde{\ell}_i - \frac{\Delta_i}{2})]^\theta - [L_\infty - (\tilde{\ell}_i + \frac{\Delta_i}{2})]^\theta}{[L_\infty - L_{\min}]^\theta - [L_\infty - L_{\max}]^\theta} \quad \dots 32)$$

$$i = 1, 2, \dots, r$$

Given $n_{\cdot}$, $L_{\min}$, and $L_{\max}$, the likelihood of the sample is therefore

$$\mathcal{L} = \binom{n_{\cdot}}{n_1 \ n_2 \ \dots \ n_r} \prod_{i=1}^r \mu_i^{n_i} \quad \dots 33)$$

and maximum likelihood estimates of L_{∞} and θ and their asymptotic standard errors may be found in the usual way by maximizing $\mathcal{L}$ or $\ln \mathcal{L}$ directly, or, for example, by fitting the expected length class frequencies to corresponding observations using an iteratively reweighted Gauss-Newton algorithm. In the latter approach, one finds θ and L_{∞} which minimize

$$\mathcal{J} = \sum_{i=1}^r \omega_i (n_i - n_{\cdot} \mu_i)^2 \quad \dots 34)$$

with weights ω_i equal to the reciprocals of the expected frequencies. The resulting maximum likelihood estimates will also be minimum chi-square estimates, and the minimized $\mathcal{J}$ will be asymptotically distributed as χ^2 with $r - 3$ degrees of freedom.

In fitting the multinomial model, a question arises concerning the optimal choice of the length classes into which the data are grouped. Intervals of equal width are customary in length-frequency analysis, but as a rule of thumb observations are often pooled where necessary to ensure an expected frequency of at least 5 in each interval. This is typically required in the right tail of the distribution. More specific guidance on grouping for a fixed number of intervals, r , may be offered if an optimality criterion is adopted. For example, one sensible choice would be to set the grouping intervals in such a way that the power of the usual multinomial chi-square goodness of fit test (or likelihood ratio test) for the null distribution is maximized with respect to some selected class of alternatives. Suppose we wish to test $g(\ell)$ against the open (unspecified) class of alternative length-frequency distributions. In this situation it has been shown (Cox and Hinkley 1974) that the optimal grouping is that which uniquely maximizes the expected "entropy" of samples drawn from the null distribution, namely,

$$I = - \sum_{i=1}^r \mu_i \log \mu_i \quad \dots 35)$$

and that this is accomplished, in our context, by dividing the length range into intervals of equal probability under $g(\ell)$. Thus the r "optimal" length class intervals should have upper end points equal to the sequence of quantiles of the length distribution, of orders $1/r, 2/r, \dots, 1$. For our multinomial model these partitions are at

$$\ell_j^* = L_{\max} - (L_{\max} - L_{\min}) \left[1 - \frac{j}{r}\right]^{\theta} \quad \dots 36)$$

$j = 1, 2, \dots, r$

In practice the unknown parameters would be replaced by estimates. We have not evaluated this procedure.

Because we would expect grouping of data to result in loss of information and reduced efficiency of estimators, the actual number of intervals used should in general be as large as possible, subject to the rule that expected frequencies in each length class exceed 4. This recommendation applies provided the assumed steady-state model is correct. In cases where recruitment is actually cyclic but the steady-state model is being used to estimate θ , simulation studies (S. Ralston, unpublished data) suggest that coarser grouping of data will have the effect of smoothing out recruitment fluctuations and increasing the precision of $\hat{\theta}$ (in the same manner that pooling of several samples taken over the course of a spawning cycle will render the steady-state model applicable). In such cases, trial and error will indicate the optimal grouping.

Systematic Biases

We turn now to a consideration of systematic biases in the estimators, which arise when the underlying model assumptions are violated. In some situations serious biases result, in others the estimation procedures are robust and biases negligible.

SUBSTITUTION OF $L_{\min}$ FOR L_c

Since L_c is a location parameter, and L_∞ a scale parameter, they have no bearing on the shape of the theoretical length distribution. This is determined solely by θ . Estimators of θ based on samples drawn randomly from (2), and assuming L_c and L_∞ are known, therefore have distributions unaffected by L_c and L_∞ , and dependent only on θ and n . However, in practice both L_c and L_∞ are unknown. In most of the procedures studied here an estimate of L_c , or of both L_c and L_∞ must be substituted, and properties of the estimators are affected.

We consider L_c first. In one of the likelihood models, the multinomial, problems related to L_c were circumvented by treating it as a nuisance parameter and conditioning the length interval probabilities on the sample end points, i.e., on $L_{\min}$ and $L_{\max}$. In all the other methods specification of L_c is required. In these cases, L_c (or w_1 in the regression method) is typically set to $L_{\min}$, the lower bound of the sample length-frequency distribution. Indeed, in most applications the frequency distribution is formed by truncating a larger sample at a selected $L_{\min}$, setting aside the data below this length, and retaining for analysis only the upper "descending" portion. Setting L_c equal to $L_{\min}$ in this manner is clearly reasonable. As pointed out in the section on Maximum Likelihood Method, doing so maximizes the likelihood of the sample under (2). Further, assuming continuous sampling (all $\Delta_i = 0$), analysis of the relevant order statistics shows that

$$E(L_{\min}) = L_c + \frac{(L_\infty - L_c)}{n\theta + 1}, \quad \dots 37$$

so that for θ greater than about 2, $L_{\min}$ is essentially unbiased as an estimator for L_c , even for fairly small samples. In virtually all cases, then, systematic biases due to estimating L_c by $L_{\min}$ will be negligible.

SUBSTITUTION OF $L_{\max}$ FOR L_∞ IN $\hat{\theta}_{BH}$ AND $\hat{\theta}_{SL}$

In the earlier sections, we noted that both $\hat{\theta}_{BH}$ and $\hat{\theta}_{SL}$ were susceptible to systematic bias resulting from the replacement of L_∞ by an independent estimate or guess. To avoid the bias, one

would need to apply one of the methods which estimate θ and L_{∞} jointly. However, heretofore only Powell's method was available for this, and we are unaware of any situations in which it has been used. In the majority of cases, one of the simpler methods has been adopted instead. Except when reliable, independent estimates of L_{∞} have been available from tagging or analysis of hard parts, the usual practice has been to set $L_{\infty} = L_{\max}$, the length of the longest fish measured, or the upper bound of the length distribution. When growth is deterministic with L_{∞} the upper bound to length, as assumed in (2), this substitution biases $\hat{\theta}_{BH}$ and $\hat{\theta}_{SL}$ downward, the degree of negative bias depending on θ , X_c , and n .

If θ is large and X_c small, very large samples are required for this systematic bias to be negligible. Specifically, under (2) it may be shown that the sample size required to ensure that $L_{\max}$ is within 100% of L_{∞} with probability ϕ is the smallest integer exceeding

$$n(\delta, \theta) = \frac{\ln(1 - \phi)}{\delta \left[1 - \left(\frac{\theta}{1 - X_c} \right) \right]} \quad \dots 38)$$

For example, if $X_c = 0.3$ and $\phi = 0.95$, we have the following results for $n(\delta, \theta)$:

δ	$\theta = 3.0$	$\theta = 4.0$
0.01	1.0×10^6	7.2×10^7
0.05	8.2×10^3	1.2×10^5
0.10	1.0×10^3	7.2×10^3
0.20	1.3×10^2	4.5×10^2

Thus for $L_{\max}$ to be a reasonably accurate estimate of L_{∞} , it must represent the longest fish in a sample of several thousand. This sample need not be the same one used to estimate θ . Indeed, if the deterministic von Bertalanffy model is correct and samples are drawn under identical conditions, $L_{\max}$ should represent the longest specimen seen in all the samples taken.

To correct for this systematic bias, it is often recommended that $L_{\max}$ be adjusted upward by some arbitrary amount, typically about 5% (e.g., Pauly 1983, who suggests dividing $L_{\max}$ by 0.95). Depending on the true value of θ and the size of the sample from which $L_{\max}$ is derived, a 5% adjustment may be a fortuitous choice, but clearly some better procedure is needed. The obvious choice, as suggested above, would be to make fuller use of the sample information to estimate θ and L_{∞} jointly, i.e., use Powell's method, the regression method, or a maximum likelihood procedure. In the same vein, an interesting alternative approach which accounts for the systematic bias explicitly is based on the following pair of equations in θ and L_{∞} , derived from (2):

$$E(\bar{l}) = L_{\infty} - (L_{\infty} - L_c) \left(\frac{\theta}{\theta + 1} \right) \quad \dots 39)$$

$$E(L_{\max}) = L_{\infty} - (L_{\infty} - L_c) \prod_{i=1}^n \left(\frac{i\theta}{i\theta + 1} \right) \quad \dots 40)$$

Substituting sample values of $\bar{l}$ and $L_{\max}$ for their expectations and solving by iteration, one can compute joint moment-type estimates of L_{∞} and θ . Sampling variances and other properties of the parameter estimates can be derived empirically using bootstrap techniques.

Numerical evaluation of the bias term in (40) shows that a simple 5% adjustment of $L_{\max}$ (or division by 0.95) is rarely appropriate (Table 1). In most fishery applications, where X_c is 0.5 or greater, the correct adjustment is apt to be anywhere between about 0.5% and 25%, depending on θ and n . The consequences of using an incorrect adjustment may be judged by various criteria, one being the so-called "D-measure" described by Majkowski (1982). For example, a D-measure analysis of $\hat{\theta}_{BH}$ shows that the estimator is quite sensitive to errors in the estimate or guess of L_∞ (Table 2). Since $\hat{\theta}_{BH}$ is linear in L_∞ , the relevant D-measure is directly proportional to the errors, and symmetrical. Combining the information in Tables 1 and 2, one can compute the expected bias in $\hat{\theta}_{BH}$ when a simple 5% upward adjustment is applied to $L_{\max}$ (Table 3). Obviously, too large an adjustment simply replaces the negative bias in $\hat{\theta}_{BH}$ with an unknown positive bias.

Table 1. Percentage negative bias in $L_{\max}$ as estimator of L_∞ , as a function of X_c , θ , and n .

X_c	n	θ		
		2.0	3.0	4.0
0.0	200	6.2	15.2	24.1
	500	4.0	11.2	19.2
	1,000	2.8	8.9	16.1
0.5	200	3.1	7.6	12.0
	500	2.0	5.6	9.6
	1,000	1.4	4.5	8.0
0.75	200	1.6	3.8	6.0
	500	1.0	2.8	4.7
	1,000	0.7	2.2	4.0

Table 2. Percentage carat, i.e., $\hat{L}_\infty$ D-measure biases in $\hat{\theta}_{BH}$ due to systematic errors in $\hat{L}_\infty$ of $\pm \delta\%$. (Biases in $\hat{\theta}_{BH}$ have same sign as errors in L_∞ .)

X_c	δ	θ		
		2.0	3.0	4.0
0.0	1	1.5	1.3	1.3
	2	3.0	2.7	2.5
	4	6.0	5.3	5.0
	8	12.0	10.7	10.0
	16	24.0	21.3	20.0
	32	48.0	42.7	40.0
0.5	1	3.0	2.7	2.5
	2	6.0	5.3	5.0
	4	12.0	10.7	10.0
	8	24.0	21.3	20.0
	16	48.0	42.7	40.0
	32	96.0	85.3	80.0
0.75	1	6.0	5.3	5.0
	2	12.0	10.7	10.0
	4	24.0	21.3	20.0
	8	48.0	42.7	40.0
	16	96.0	85.3	80.0
	32	192.0	170.7	160.0

Table 3. Percentage bias in $\hat{\theta}_{BH}$ when L_∞ is set at $L_{\max}/0.95$, under various combinations of X_c , θ , and n .

X_c	n	θ		
		2.0	3.0	4.0
0.0	200	-1.9	-14.3	-25.1
	500	+1.6	-8.7	-18.7
	1,000	+3.5	-5.5	-14.6
	∞	+7.9	+7.0	+6.6
0.5	200	+6.0	-7.3	-18.4
	500	+9.5	-1.7	-12.1
	1,000	+11.4	+1.4	-7.9
	∞	+15.8	+14.0	+13.2
0.75	200	+21.5	+6.7	-5.3
	500	+25.3	+12.3	+1.6
	1,000	+27.2	+15.7	+5.3
	∞	+31.6	+28.1	+26.3

VARIABILITY IN ASYMPTOTIC LENGTH

Another problem of systematic bias can arise if $L_{\max}$ is substituted for L_{∞} in the Beverton-Holt or Ssentongo-Larkin formulas but the deterministic von Bertalanffy model is incorrect. Specifically, if the growth trajectories of individual fish converge on different asymptotic lengths, i.e., if $\sigma_{\lambda}^2 > 0$, $L_{\max}$ can easily exceed the expected asymptotic length, L_{∞} , when derived from large samples. As Powell's model shows, the positive bias in $L_{\max}$ as an estimator of L_{∞} can be significant when σ_{λ}^2 is relatively large and θ is not. Subsequent estimates of θ will also be inflated.

Under such conditions, the maximum likelihood methods based on (2) will also give biased results, since $L_{\max}$ is regarded as a lower bound on $\hat{L}_{\infty ML}$. Partial remedies might be to base estimation on the more realistic likelihood arising from the stochastic model of Powell, or to estimate L_{∞} by some statistic reflecting the average size of the largest fish seen in the catches. Using Powell's likelihood would entail estimation of σ_{λ}^2 as well as θ and L_{∞} , and would require numerical approximation of the theoretical length frequencies.

We note that because the regression method at (19) is based on fitting sample mean lengths to their expected values, which are unaffected by σ_{λ}^2 , the estimates of L_{∞} it produces do not suffer from these types of bias. In contrast, Powell's estimators of θ and L_{∞} are derived assuming $\sigma_{\lambda}^2 = 0$, so are presumably biased when this assumption is violated.

VARIABLE RECRUITMENT

Variability in recruitment violates a basic assumption of the methods, but is not particularly troublesome as long as the process is stationary, i.e., there has been no systematic trend in R . When spawning is periodic and reasonably regular, and survival of pre-recruits is stable, the effects of variable recruitment can be smoothed out by sampling the population on several occasions during a complete spawning cycle and pooling the individual length-frequency distributions. Distributions should be weighted by an index of population size, such as average catch per unit effort. When recruitment is trending up or down the smoothing procedure is ineffective, and serious bias in estimates of θ can result from use of any of the estimators, the bias being in the same direction as the trend in R .

VARIABLE MORTALITY

If the simple, constant mortality models are applied to length-frequency data when in fact mortality is variable, subsequent population assessments and yield computations based on the estimates of θ and L_{∞} are likely to be biased. But since the robustness of the methods in such circumstances has not been studied, the specific ramifications are unclear.

Nevertheless, several forms of variability may be identified, and some are more easily handled than others. One kind is temporal variability in mortality, caused, for example, by a systematic change in fishing effort or stock vulnerability. Accommodating this kind of variability would be relatively difficult, because the simplifying steady state conditions no longer exist. A second type of variation is that due to size (or age) dependence of mortality. Assuming such size-specificity is time invariant, construction of steady-state population models and parameter estimation procedures is straightforward. We develop such procedures in the following section.

Estimating Length-Specific Fishing Mortality Rates

When aging of the catch is feasible, the analysis of cohort catch histories is one of the chief methods of estimating virtual populations and age-specific mortality rates. When it is not, but the

catch is known by length class interval, one may estimate population size and length-specific mortality using a length-based analog of the cohort methods (e.g., Jones 1981; Pauly 1984). These are applicable under more restrictive assumptions than cohort analysis. Recruitment must be approximately constant, or smoothed out by pooling catch-at-length data, a growth model must be assumed, and mortality rates must be constant in time.

The method developed by Jones and extended by Pauly is based on the deterministic von Bertalanffy growth model and a constant instantaneous natural mortality rate, M . Assuming M , the fishing mortality rate in the largest length class, F_r , and the von Bertalanffy parameters K and L_∞ are known, the length-based VPA proceeds recursively in the same manner as the popular age-based methods, beginning with the catch in the largest length class and working backward to estimate the sequence of length-specific population sizes and fishing mortality rates. Alternatively, if only L_∞ and the "exploitation rate" F_t/Z_t in the terminal length class are specified (where $Z_t = F_t + M$), estimates of M/K and the remaining F_i/Z_i may be found, there being in either case one parameter estimated for every data point, i.e., every length-interval catch.

In this section we adopt the same steady-state assumptions, and describe an alternative procedure for estimating length-specific mortality rates, growth parameters and population size jointly from a regression analysis of catch by length class. This is simply an extension of the age-based catch curve models developed by Ricker (1948, 1975) and frequently applied to cohort analysis.

Historically, in fact, the age-based catch curves were preceded by length-based methods due to Edser (1908), Heincke (1913), and Baranov (1918).

We assume a steady state, with constant recruitment, R , constant natural mortality rate M , and knife-edge selection at age t_c . Beyond t_c , the fishing mortality rate F is described as a step function of age t , namely

$$F(t) = F_i \quad \dots 41)$$

$$t_i < t < t_i + \delta_i$$

$$i = 1, 2, \dots, r$$

where $t_i = t_c + \sum_{j=1}^i \delta_{j-1}$ and the δ s are successive age increments ($\delta_0 = 0$). Under these conditions, the number of fish caught in the i -th age class, $(t_i, t_i + \delta_i)$, during a time period of duration τ , is

$$\begin{aligned} C(t_i, t_i + \delta_i) &= R\tau \left(\frac{F_i}{F_i + M} \right) \left(1 - e^{-(F_i + M)\delta_i} \right) e^{-\sum_{j=1}^i (F_{j-1} + M)\delta_{j-1}} \quad \dots 42) \\ &= C_i, \text{ say.} \end{aligned}$$

Let the δ_i correspond, by virtue of a bijective growth model, to a specific sequence of length intervals into which the catch is conveniently grouped, say the sequence $(w_i, w_i + \Delta_i)$, $i = 1, 2, \dots, r$,

where $w_i = L_c + \sum_{j=1}^i \Delta_{j-1} = \tilde{L}_i - \Delta_i/2$ and $\Delta_0 = 0$. If the von Bertalanffy model is used, the correspondence is established by the relation

$$\delta_i = -\frac{1}{K} \ln \left\{ \frac{L_\infty - (w_i + \Delta_i)}{L_\infty - w_i} \right\} \quad \dots 43)$$

Making the substitution of length for age, we have

$$C_i = R\tau \left(\frac{F_i}{Z_i} \right) \left[1 - \left(\frac{L_\infty - (w_i + \Delta_i)}{L_\infty - w_i} \right)^{\theta_i} \right] \prod_{j=1}^i \left(\frac{L_\infty - (w_{j-1} + \Delta_{j-1})}{L_\infty - w_{j-1}} \right)^{\theta_{j-1}} \quad \dots 44)$$

where $Z_i = F_i + M$, $\theta_i = Z_i/K$, and $w_0 = \Delta_0 = Z_0 = 0$.

If the fishing mortality rate is constant after recruitment, (44) reduces to

$$\begin{aligned} C_i &= R\tau \left(\frac{F}{Z} \right) \left[1 - \left(\frac{L_\infty - (w_i + \Delta_i)}{L_\infty - w_i} \right)^{\theta} \right] \left(\frac{L_\infty - w_i}{L_\infty - L_c} \right)^{\theta} \quad \dots 45) \\ &= C \cdot \left[\frac{(L_\infty - w_i)^{\theta} - (L_\infty - (w_i + \Delta_i))^{\theta}}{(L_\infty - L_c)^{\theta}} \right] \end{aligned}$$

where $C/\tau = R F/Z$ is the constant total catch in a unit time interval. Alternatively, (45) may be derived from the length density at (2), i.e.,

$$\begin{aligned} C_i &= \tau F \int_{w_i}^{w_i + \Delta_i} N(\ell) d\ell \quad \dots 46) \\ &= \tau F \frac{R}{Z} \int_{w_i}^{w_i + \Delta_i} g(\ell) d\ell \\ &= C \cdot [G(w_i + \Delta_i) - G(w_i)] \end{aligned}$$

where $N(\ell)$ is the number of fish of length ℓ in the steady-state population. Recalling the earlier discussion on maximum likelihood methods, C_i/C is seen to be the probability that a fish taken at random from the population will be in the i -th length class interval, a function of L_c , L_∞ , and Z/K , as in (29).

As formulated in (44), the length-based catch model is a set of r equations in $r + 4$ unknown parameters (R , M , K , L_∞ , and the F_i , $i = 1, 2, \dots, r$), so additional restrictions must be imposed to permit estimation. As usual, this may be done by making further structural assumptions about fishing mortality. One possibility is to assume that fishing mortality rates are constant and distinct

within $m < r - 4$ segments of the catchable length range. Another is to relate fishing mortality rate to length class by a particular parametric model, such as the quadratic $F(i) = a + bi + ci^2$. In the latter event the problem is reduced to estimating seven parameters from the r observed length class catches.

With proper structuring, so that adequate degrees of freedom are available, the q -model parameters can be estimated by iteratively reweighted least squares. When weights are set equal to the expected catches, this amounts to minimizing the familiar Pearson chi-square statistic. For large samples, this statistic will be distributed as χ^2 with $r - q - 1$ degrees of freedom. The resulting parameter estimates will also be maximum likelihood estimates, and if a Gauss-Newton algorithm is used in the optimization an estimate of their asymptotic covariance matrix will be readily available.

For some purposes individual estimates of M , K and the fishing mortality rates may not be necessary, and in this event the catch models can be parameterized in terms of R , L_∞ , and the ratios M/K and F_i/Z_i , $i = 1, 2, \dots, r$. (In the structured mortality model, let $F_i/Z_i = a' + b'i + c'i^2$). In (44), for example, this is accomplished by replacing θ_i by the product

$$\theta_i = \left(\frac{M}{K} \right) \left(1 - \frac{F_i}{Z_i} \right)^{-1} \quad \dots 47)$$

In the models just described, it is assumed that the entire catch is taken by a single gear, so that estimating the length-specific fishing mortality rates is equivalent to estimating the selectivity curve for that gear with respect to the species under study. If more than one gear is significantly involved, then the catch data from all of them must be combined (properly weighted), and the analysis applied to the aggregate information. As in age-based VPA methods, gear-specific fishing mortality rates can be computed by allocating the fishing mortality estimate for each length class in proportion to the associated catch by each gear.

We have not yet applied these procedures, nor investigated their robustness and other properties. Nevertheless, we would speculate that length-specific fishing mortality rates will not be identifiable, or estimable with much precision, unless they vary fairly dramatically with length. Further, separation of natural mortality and the fishing mortality rates and useful precision in the mortality rate estimates will likely require that a substantial fraction of the total mortality be due to fishing. Thus, the model will probably not estimate fishing mortality rates well when applied to lightly exploited stocks.

However, when adequate length-frequency data are available from virgin populations or very lightly exploited stocks, a regression model may be developed to estimate L_∞ , K and a set of length-specific natural mortality rates. Taking C_i to be a small sample proportional to τ and the steady state population size in the i -th length class, we will have, corresponding to (44), the model

$$C_i = \delta \left(\frac{R\tau}{M_i} \right) \left[1 - \left(\frac{L_\infty - (w_i + \Delta_i)}{L_\infty - w_i} \right)^{\frac{M_i}{K}} \right] \quad \text{for } i = 1, \dots, j \quad \left(\frac{L_\infty - (w_{j-1} + \Delta_{j-1})}{L_\infty - w_{j-1}} \right)^{\frac{M_{j-1}}{K}} \quad \dots 48)$$

where δ is the proportionality constant and M_i is the instantaneous natural mortality rate in the i -th length interval. Again, further restrictions on the parameters are necessary to allow estimation. Structural relationships among the M_i could be introduced, as above. If the segmented mortality model is adopted, such independent information as average size at maturity could be used to define points of change in the model. Note that the steady-state recruitment level, R , is no longer estimable, and difficulty in estimating the mortality parameters can be expected unless the length-specific changes in mortality rate are striking. When variation in natural mortality rates is negligible, only L_∞ and $\theta = M/K$ are estimable from the length-frequency information.

Evaluation of Methods

Four of the constant-mortality methods described above were compared by Monte Carlo procedures in situations where both θ and L_∞ were to be estimated from length-frequency data and L_c was assumed known. Specifically, performance of the following procedures was examined:

- (i) L_∞ was set equal to $L_{\max}$, and the classical Beverton-Holt estimator then applied to estimate θ .
- (ii) Powell's method of moments was applied to estimated L_∞ and θ , given the sample mean and variance of ℓ .
- (iii) The weighted regression method, based on the linear relationship between $\bar{\ell}$ and L_c , was used to estimate L_∞ and θ .
- (iv) The continuous maximum likelihood method was applied to estimate L_∞ and θ .

For specified values of X_c and θ samples of lengths were drawn from (6) by the inverse transformation method, a well-known Monte Carlo procedure. Let u be a random variate uniformly distributed on $(0, 1)$. Then a corresponding random variate from (6), x , is uniquely determined by

$$x = 1 - (1 - X_c) (1 - u)^{\frac{1}{\theta}} \quad \dots 49)$$

A uniform random number generator was used to produce sets of u_i and the associated random lengths, x_i , $i = 1, 2, \dots, n$. Except when the level of aggregation was being studied, experiments were conducted using the raw generated lengths. Thus a continuous distribution of the sample variates was assumed (all $\Delta_i = 0$). Recall that use of the auxiliary variable, X , is equivalent to scaling the length axis so that $L_\infty = 1.0$.

Performance of the estimators was measured by the coefficient of variation (CV), the relative bias (B), and the coefficient of error (CE). For a particular parameter π , we define these as

$$CV(\hat{\pi}) = \frac{\sqrt{\text{var}(\hat{\pi})}}{\pi}, \quad \dots 50)$$

$$B(\hat{\pi}) = \frac{\text{Bias}(\hat{\pi})}{\pi}, \quad \dots 51)$$

and

$$CE(\hat{\pi}) = \sqrt{CV(\hat{\pi})^2 + B(\hat{\pi})^2} = \frac{\sqrt{\text{MSE}(\hat{\pi})}}{\pi} \quad \dots 52)$$

where $\text{MSE}(\hat{\pi})$ is the mean squared error of $\hat{\pi}$. For each set of experimental circumstances, these measures were computed with respect to L_∞ and $\hat{\theta}$ on the basis of 200 replicate samples. Trial simulations showed that this number of replicates was sufficient to describe the sampling distributions of the estimators accurately.

Experimental variables of primary interest were the level of θ and the sample size, n . Of lesser interest were $1 - X_c$, the proportion of the total possible length range selected in the sample, the level of aggregation in the data, and, in the regression method, the number of partitions and type of weighting used. Below we describe each particular simulation experiment, and the chief results.

Experiment 1

The performance of the four estimation procedures was compared at three levels of θ (2.0, 3.0, 4.0) and three levels of n , (200, 500, 1,000), with $X_c = 0$.

Results: The Beverton-Holt method produces estimates with the lowest CV, but these estimates have a substantial negative bias, especially with small n , and large θ (Tables 4 and 5). The Powell method, on the other hand, computes estimates with the highest CV of any method examined, but generally with the smallest B (positive) as well. Estimates derived by the regression

Table 4. Performance measures for various estimators of L_∞ , as a function of θ and n .

n	Method	CV	θ			CV	θ			CV	θ		
			2.0	B	CE		3.0	B	CE		4.0	B	CE
200	BH	3.3	-5.9	6.8	6.1	-15.3	16.5	7.1	-23.2	24.3			
	P	10.7	2.1	10.9	15.9	1.8	16.0	39.5	12.4	41.4			
	R	5.8	-1.0	5.9	10.3	-5.3	11.6	19.2	-7.2	20.5			
	ML	4.7	-1.7	5.0	10.5	-3.2	11.0	25.2	3.7	25.4			
500	BH	2.2	-3.7	4.3	4.0	-11.4	12.1	5.8	-19.2	20.1			
	P	6.6	0.8	6.6	11.2	1.7	11.3	13.0	1.3	13.0			
	R	3.4	-0.4	3.4	6.6	-1.9	6.9	11.1	-4.2	11.9			
	ML	2.6	-0.7	2.7	6.0	-1.1	6.1	9.6	-1.5	9.7			
1,000	BH	1.7	-2.7	3.2	3.5	-8.6	9.3	4.6	-16.7	17.3			
	P	4.6	-0.1	4.6	7.3	1.2	7.4	11.6	0.8	11.7			
	R	2.4	-0.4	2.4	5.0	-0.8	5.1	7.9	-3.8	8.8			
	ML	1.8	-0.6	1.9	4.5	-0.2	4.5	7.5	-1.5	7.7			

Table 5. Performance measures for various estimators of θ , as a function of θ and n .

n	Method	CV	θ			CV	θ			CV	θ		
			2.0	B	CE		3.0	B	CE		4.0	B	CE
200	BH	8.7	-9.0	12.5	8.8	-20.3	22.2	9.7	-28.5	30.1			
	P	20.0	3.5	20.3	24.0	3.0	24.2	54.8	17.5	57.5			
	R	12.2	-3.0	12.6	16.7	-8.0	18.5	28.6	-9.0	30.0			
	ML	12.2	-3.0	12.6	17.3	-4.3	17.9	36.3	5.8	36.8			
500	BH	5.0	-5.0	7.1	5.8	-15.0	16.1	7.5	-23.8	24.9			
	P	12.2	1.5	12.3	17.0	3.0	17.3	18.0	2.0	18.1			
	R	7.1	-0.5	7.1	10.5	-2.7	10.9	16.4	-4.8	17.1			
	ML	7.1	-1.0	7.1	10.5	-1.3	10.6	13.9	-1.5	14.0			
1,000	BH	5.0	-4.0	6.4	5.8	-10.7	12.1	6.1	-20.7	21.6			
	P	8.7	-0.5	8.7	11.1	2.3	11.3	15.4	1.3	15.5			
	R	5.0	-1.0	5.1	8.2	-0.3	8.2	10.6	-5.0	11.7			
	ML	5.0	-1.0	5.1	7.5	0.3	7.5	10.3	-2.0	10.5			

method, with optimal weighting and 10 partitions, appear to have slightly greater bias than the maximum likelihood estimates (negative in both cases) and the Powell method, but are far superior to the Beverton-Holt estimates in this regard. In terms of precision, the regression method is almost as good as the maximum likelihood method.

As expected, the maximum likelihood method, among the estimators examined, generally has the best overall performance in terms of mean squared error and CE, followed closely by the regression method. The maximum likelihood estimates of L_{∞} almost always had the smallest CE. At $\theta = 2$, the Beverton-Holt procedure performed relatively well in terms of CE, virtually on a par with the maximum likelihood and regression methods, but it did comparatively poorly at higher values of θ . At $\theta = 2$, the Powell estimates generally had the largest CE of any method; otherwise, Beverton-Holt estimates tended to have the largest CE.

In all methods, the effect of increasing θ is to increase B, CV, and CE for both parameters estimated. As expected, increasing n , uniformly reduces B, CV, and CE.

Experiment 2

The effects on Beverton-Holt estimates of using a bias-corrected estimate of L_{∞} were studied. In each generated sample, $L_{\max}$ was increased by the theoretical bias term on the right side of (40), and this corrected estimate of L_{∞} was used as a basis for estimating θ .

Results: Adjustment of $L_{\max}$ for bias resulted in a significant reduction in B ($\hat{L}_{\infty \text{ BH}}$), as anticipated, and also in B ($\hat{\theta}_{\text{BH}}$), and increases in CV for both parameter estimates. The CE's were changed very little by the adjustment. In practice, the bias correction procedure would have to be implemented by iterative solution of (39) and (40), i.e., the bias term itself would have to be estimated, and the properties of the estimators would be affected.

Experiment 3

The effects of X_c on the performance of all methods was studied, with n , fixed at 200, and θ at 3.0. Samples were drawn from (6) with X_c set at three levels (0.0, 0.5, 0.75) and estimators were applied with X_c assumed known.

Results: As expected, increasing the value of X_c (with n , unchanged) reduced B, CV, and CE for L_{∞} in all methods, but had no effect on estimates of θ . With respect to estimation of L_{∞} , increases in X_c have the same effect as increasing sample size with X_c fixed. On the other hand, as pointed out earlier, distributions of $\hat{\theta}$ are unaffected by the magnitude of X_c when X_c is known. The amount of information about θ conveyed by the sample depends only on θ and the sample size. (Note, for example, that in the regression model if L_c is known, θ is completely determined by the slope of the regression line, the expected value of which is independent of X_c .)

Experiment 4

The effects of weighting schemes and the number of partitions on estimates produced by the regression method were studied. Weights were determined in three ways: (1) the complete covariance matrix was inverted, (2) the diagonal elements only were inverted, and off diagonal elements neglected and (3) uniform weights were assigned. Under the diagonal weighting scheme, regression estimates were computed with both 10 and 20 partitions.

Results: Use of the full covariance weighting produced the most precise estimates, as expected, but these estimates had greater bias than those produced with either diagonal or uniform weighting. However, the fully weighted estimates had the lowest CEs. When 10 partitions are used, diagonal weighting, or even equal weighting, appears to be satisfactory.

Similarly, increasing the number of partitions (points) in the regression reduced the CVs at the expense of greater bias and resulting estimates had smaller CEs.

Experiment 5

Effects of aggregation were assessed by comparing estimates derived using continuous data (i.e., exact lengths) with those computed from data grouped by intervals of width $L_\infty/100$.

Results: In most cases, aggregation at this level slightly increased the CVs and reduced relative biases (except for increases in bias of Powell estimates). The CEs were increased slightly in all methods except the Beverton-Holt, in which case they were reduced. (Note that among the estimators studied, those of the Beverton-Holt procedure are distinguished by having their CEs composed mostly of bias. In the other methods, the variance dominates.)

Conclusions and Recommendations

Each of the methods outlined here has attributes which make it the method of choice in particular circumstances.

The classical estimator of θ due to Beverton and Holt, for example, is the only one applicable when the available information is limited to the mean length in a sample of fish above L_c and an independent estimate of L_∞ . The difficulty with the method, of course, is that considerable bias in $\hat{\theta}_{BH}$ will result unless L_∞ is known accurately. As discussed earlier, estimating L_∞ by $L_{\max}$ is advisable only if a very large sample has been measured. Alternatively, the estimate of L_∞ (and K) can be derived independently by fitting the von Bertalanffy model to tag recapture data or to readings of hard parts, and then substituted into the Beverton-Holt estimator. Here, too, L_∞ is rarely determined with sufficient accuracy unless fish are aged, or tagged and recovered, over the entire length range and an asymptote is clearly evident. These conditions are difficult to achieve when there is a low probability that a tagged fish will survive long enough to approach the asymptotic length and be recaptured, or when otoliths and other hard structures are difficult to read and interpret in old fish. The result is often serious bias in estimates of L_∞ and K . However, since these biases are inversely related, some compensation occurs when the pair of parameter estimates is inserted into the Beverton-Holt formula to compute Z .

If the variance among lengths in the sample is known in addition to the mean, a considerable improvement is afforded by Powell's method of moments, which provides joint estimates of θ and L_∞ without reliance on independent information. If tag recapture statistics or otolith data are available, they may then be used to estimate K with L_∞ fixed at $L_{\infty p}$. An estimate of Z follows immediately.

The weighted regression method is attractive for several reasons, and has proven to be the most dependable of the constant-mortality methods in practice. In statistical terms, it is very efficient, giving parameter estimates with almost minimum mean squared error. It also is insensitive to assumptions on L_∞ , which may be regarded either as an absolute upper bound to length, or as the expected asymptotic length in a stochastic von Bertalanffy growth process. Among the simple methods studied, only the Beverton-Holt procedure shares this robustness with respect to L_∞ .

Another reason for recommending the regression method is that it provides a simple graphical means of judging the appropriateness of underlying model assumptions; serious violations can be detected directly by comparing observed mean lengths above the specified cut-off points with those predicted by the model.

Perhaps the only drawback to the regression method is the need to compute the covariance matrix A to achieve full efficiency. However, little is sacrificed by weighting simply by the partition sample sizes.

From a theoretical standpoint, the maximum likelihood procedure is highly attractive, yielding estimators with greatest asymptotic efficiency and other desirable properties. However, it is not robust to violations of the assumption on L_∞ , and this has apparently been a source of difficulty in applications. In a number of cases, searches for L_∞ have converged on $L_{\max}$, suggesting overestimation of L_∞ and θ . Use of Powell's stochastic model (or a suitable variant) in a maximum likelihood context might be more appropriate, but we have not tried it.

In the methods outlined here, estimators are based on length-frequency data entirely, or on combinations of length-frequency data and other information, applied sequentially. Where consistent information on growth and mortality is available from several independent sources, e.g., from tagging, otolith analysis or length-frequency samples, it may also be used jointly to estimate the parameters of a common steady-state model. A maximum likelihood approach is most appropriate here, provided one can specify the forms of the various error distributions. An ancillary benefit of joint estimation is that the relative contribution of each type of information toward the mean squared errors of the parameter estimates can be determined, providing useful guidance for research planning and allocation of resources. Examples of joint estimation of growth parameters from length-increment data and age-length data have been reported by Laurs et al. (1983), who combined tag recapture results with counts of daily increments on sagittae of North Pacific albacore, by Kirkwood (1983), who pooled tag recapture data with information on "aged" length-frequency modes in southern bluefin tuna and by Morgan (Part I, this vol.). Extension of such techniques to joint estimation of growth, mortality and recruitment parameters in more general contexts is straightforward.

References

- Baranov, F.I. 1918. On the question of the biological basis of fisheries. Nauchn. Issled. Ikhtiol. Inst. Izv. 1: 81-128. (In Russian.)
- Beverton, R.J.H. and S.J. Holt. 1956. A review of methods for estimating mortality rates in fish populations, with special reference to sources of bias in catch sampling. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 140: 67-83.
- Cox, D.R. and D.V. Hinkley. 1974. Theoretical statistics. Chapman and Hall, London.
- Edser, T. 1908. Note on the number of plaice at each length, in certain samples from the southern part of the North Sea, 1906. J.R. Stat. Soc. 71: 686-690.
- Gulland, J.A. 1983. Fish stock assessment: a manual of basic methods. FAO/Wiley Series on Food and Agriculture.
- Heinke, F. 1913. Investigations on the plaice. General report. 1. Plaice fishery and protective regulations. Part I. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 17A: 1-153.
- Jones, R. 1981. The use of length composition data in fish stock assessments (with notes on VPA and cohort analysis). FAO Fish. Circ. 734. 60 p.
- Kirkwood, G.P. 1983. Estimation of von Bertalanffy growth curve parameters using both length-increment and age-length data. Can. J. Fish. Aquat. Sci. 40: 1405-1411.
- Laurs, R.M., R. Nishimoto, J.H. Uchiyama and J.A. Wetherall. 1983. Age and growth of North Pacific albacore, *Thunnus alalunga*, determined from tag returns and daily increments on otoliths. Eighth North Pacific Albacore Workshop, Document NPALB/83/1. National Marine Fisheries Service, Southwest Fisheries Center Admin. Report LJ-84-04.
- Majkowski, J. 1982. Usefulness and applicability of sensitivity analysis in a multispecies approach to fisheries management, p. 149-165. In Pauly, D and G.I. Murphy (eds.) Theory and management of tropical fisheries. ICLARM Conference Proceedings 9, 360 p. International Center for Living Aquatic Resources Management, Manila, Philippines and Division of Fisheries Research, Commonwealth Scientific and Industrial Research Organisation, Cronulla, Australia.
- Pauly, D. 1983. Some simple methods for the assessment of tropical fish stocks. FAO Fish. Tech. Pap. 234, Rome, 52 p.
- Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Studies and Reviews 8, 325 p. International Center for Living Aquatic Resources Management, Manila, Philippines.
- Pauly, D. and N. David. 1981. ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequency data. Meeresforsch. 28: 205-211.
- Powell, D.G. 1979. Estimation of mortality and growth parameters from the length frequency of a catch. Rapp. P.-v. Réun. Cons. Int. Explor. Mer 175: 167-169.
- Ricker, W.E. 1948. Methods of estimating vital statistics of fish populations. Indiana Univ. Publ. Sci., Ser. 15, 101 p.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull., 191, 382 p.
- Schnute, J. and D. Fournier. 1980. A new approach to length-frequency analysis: growth structure. Can. J. Fish. Aquat. Sci. 37: 1337-1351.
- Ssentongo, G.W. and P.A. Larkin. 1973. Some simple methods of estimating mortality rates of exploited fish populations. J. Fish. Res. Board Can. 30: 698-698.

THE IMPACTS OF ESTUARINE DEGRADATION AND
CHRONIC POLLUTION ON POPULATIONS OF ANADROMOUS
STRIPED BASS (*MORONE SAXATILIS*) IN THE
SAN FRANCISCO BAY-DELTA, CALIFORNIA: A SUMMARY

Jeannette A. Whipple, R. Bruce MacFarlane
Maxwell B. Eldridge, and Pete Benville, Jr.
Tiburon Fisheries Laboratory
NOAA/National Marine Fisheries Service

Introduction

When most of us think of pollution effects on the marine environment, we are likely to think of dramatic events such as major tanker accidents and oil spills, or fish kills resulting from sewage effluents and toxic spills. These incidents are highly visible and receive considerable public attention. There is no doubt that such occurrences are damaging to the marine environment and warrant concern about the protection of that environment.

Unfortunately, we may be deluded into thinking that if we prevent or ameliorate damage from such catastrophic events, our pollution problems have been solved. If we do this, we overlook a potentially greater problem -- that is continual or chronic input of pollutants at lower levels. For example, in the 1960s, there was considerable activity leading to decreased sewage pollution of San Francisco Bay. This was certainly commendable, but also led to the impression that our pollution problems were over. Little attention was paid to the less visible and potentially more harmful effects of increasing pollution from "water-soluble" chemicals.

The long-range effects of chronic exposure to pollutants on our aquatic resources are still relatively unknown. Levels of pollutants, in this situation, are lower but more prevalent. Effects, if they occur, are more subtle, yet the damage to our resources may be considerable and, in many cases, irreversible.

It is difficult to study effects of chronic pollution for a number of reasons. First, most marine ecosystems potentially impacted by pollutants are inherently complex and variable in space and time. Many ecosystems are described incompletely, either qualitatively or quantitatively, and even under completely natural conditions. Natural perturbations may exceed those induced by man's influence. For example, in 1983 the El Nino off the coast of California resulted in warm water conditions and significant alterations in distribution and survival of coastal fishes. This makes it very difficult to detect alterations in the environment ascribable to pollution, and even harder to predict them.

A second difficulty arises from the complex array of different pollutants occurring in the marine environment, particularly in estuarine ecosystems such as San Francisco Bay-Delta, which are most affected by man.

Finally, sublethal effects of low pollutant concentrations on organisms are subtle and difficult to quantify on an individual or population level; their detection also may be obscured by inherent species variability such as age, sex, or genetic differences.

A solution to this intricate problem requires a long-term, cooperative effort. The goal of the Physiological Ecology Investigation at Tiburon Laboratory has been to contribute to an understanding of the long-term ecological consequences of pollutant effect on aquatic resources. Specifically, we were concerned with developing knowledge of effects of chronic low-level pollutants on fisheries. Although the understanding of fate and effects of pollutants in the marine environment has increased in the past 20 years, this knowledge is still limited primarily to acute effects of single pollutants or pollutant classes. Little is known of chronic, interactive effects of pollutants within and between pollutant classes. Most effects studies are limited to the laboratory; little information exists on the quantitative effect of pollutants on a population level. Finally, few studies address the interactions of pollutants with inherent characteristics of the species or with other environmental factors.

In order to to describe source of variability in pollutant effects on striped bass more completely, we used techniques of multivariate analysis similar to those used in epidemiology. We were then able to refine the data to determine the best methods for measuring pollutant effects in both the field and in laboratory experiments.

Our approach concentrated on "easy to measure" and/or "sensitive" characteristics of the organisms which appeared to correlate with pollutant burdens. Initially, the measurements were on several levels -- from the biochemical to the subsample (population) level. After preliminary studies, the most sensitive variables were delineated. Selected groups of variables (factors) were then designated as measures of body conditions, liver condition, and egg condition. Eventually, these factors coefficients were translated into an overall assessment of the health of the organism. The coefficients also can be used to estimate quantitative effects on a population level, such as reductions in growth, reproduction, and survival. Some of the measurements are also more sensitive and consequently more effective in giving us an early warning that individuals and/or the population are stressed. Ultimately, we hope to synthesize the results into a model of the impacts of long-term chronic pollution on "natural" mortality rates and resulting changes in the population of the affected fishery.

The following questions were asked when formulating our research plans. In this summary, the questions are placed within the context of the Office of Marine Pollution Assessment* Research Program Conceptual Organization (Figure 1):

Anthropogenic Activities

1. Which pollutants are potentially impacting our marine resources, including fisheries?
2. What are the sources of these pollutants?

Marine Ecosystem Processes

3. What are the interactive effects of the pollutants on fishes? How are they related to other ecosystem processes, such as variation in outflow and diversion?

Consequences Attribute to Anthropogenic Activities

4. Are there effects on fish attributable to chronic pollutant exposures?
5. If so, what are the effects and which measurements provide the most sensitive and specific assessment of them?
6. Are the effects reversible? Are there either short-term or long-term irreversible effects on individuals and populations?

Judgemental Processes

7. What are the quantitative reductions in populations in growth, reproduction, and survival attributable to pollutants?
8. Can these effects be predicted?
9. What recommendations based on our results can be made to management and regulators for the decisions necessary to regulate anthropogenic activities deleteriously affecting fisheries?

Other Compartments

10. Other compartments in the conceptual representation

Figure 1 are within the purview of management

*OMPA is now the Ocean Assessment Division of the National Oceanic and Atmospheric Administration (NOAA).

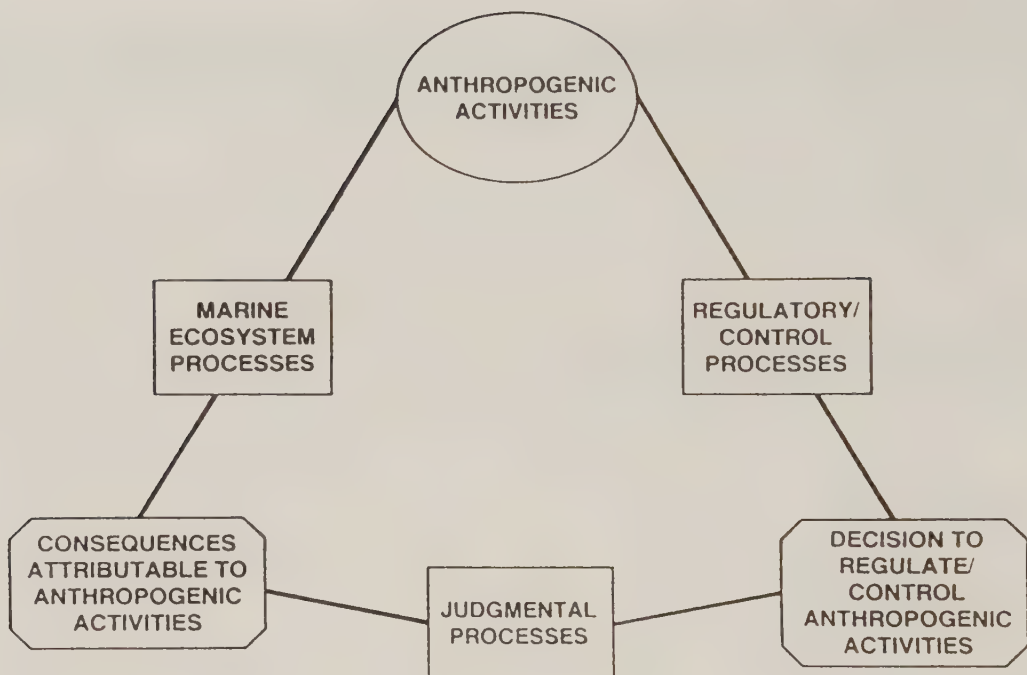


Figure 1. Conceptual representation of Office of Marine Pollution Assessment Research Program. From R.E. Burns, January 19, 1982. "Office of Marine Pollution Assessment (OMPA) Financial Assistance for Marine Pollution Research."

In June 1980, the Cooperative Striped Bass Study (COSBS) team was organized to examine different aspects of the above questions (Jung and Bowes, 1980; Jung et. al. 1981; Whipple, Crosby, and Jung, 1983; Whipple et. al. 1984; Jung, Whipple, and Moser, 1984).

At the Tiburon Laboratory, we concentrated on the affects of pollutants on striped bass populations (4 through 8, above). From this research, a number of recommendations have been made (9 above). The State Water Resource Control Board (SWRCB) stressed work on the anthropogenic sources of pollutants found in the striped bass and identification of the pollutants (1 and 2 above), funded additional studies on effects of pollutants and parasites, (4 through 8), and took a number of management actions (10 above). The California Department of Fish and Game (CDFG) also participated in management decisions (10 above).

There were a number of excellent reasons for selecting the striped bass as a model species in the San Francisco Bay-Delta ecosystem. The striped bass is a long-lived fish (approximately 20 years) and at all ages appears to accumulate relatively high levels of pollutants. It is a tertiary carnivore and accumulates pollutants throughout the food chain. Striped bass are also very euryhaline, occurring in offshore marine areas, estuaries, and in freshwater. They occur on all coasts of the United States and have been introduced in other countries. This fishery is also of great commercial and recreational value.

The major reason for studying striped bass, however, was the long-term decline on this population in the area, as well as in most other estuaries of the United States. We suggest that at least part of the decline may be because of the interactive deleterious effects of anthropogenic factors, such as water diversion and pollution.

California Department of Fish and Game (CDFG) biologists have studied the striped bass population in the San Francisco Bay-Delta estuary for about 40 years. Their work provided the framework for studies of this species, particularly in the field. The initial results of CDFG studies revealed a high correlation between outflow from the Delta and survival of striped bass to "young-of-the-year" or juvenile stage. A correlation also existed between the percentage of water diverted south through the California aqueduct system and survival of juveniles. On the basis of these correlations, CDFG was able for some years to predict survival of juveniles and recruitment to the fishery. These predictions became less reliable in later years (since approximately 1975), although outflow and diversion remain major controlling factors in survival. Figure 2A shows the decline in survival to juvenile striped bass in both the Suisun Bay and central Delta nursery areas; Figure 2B shows the decline in adult striped bass (from Stevens et. al. 1985).

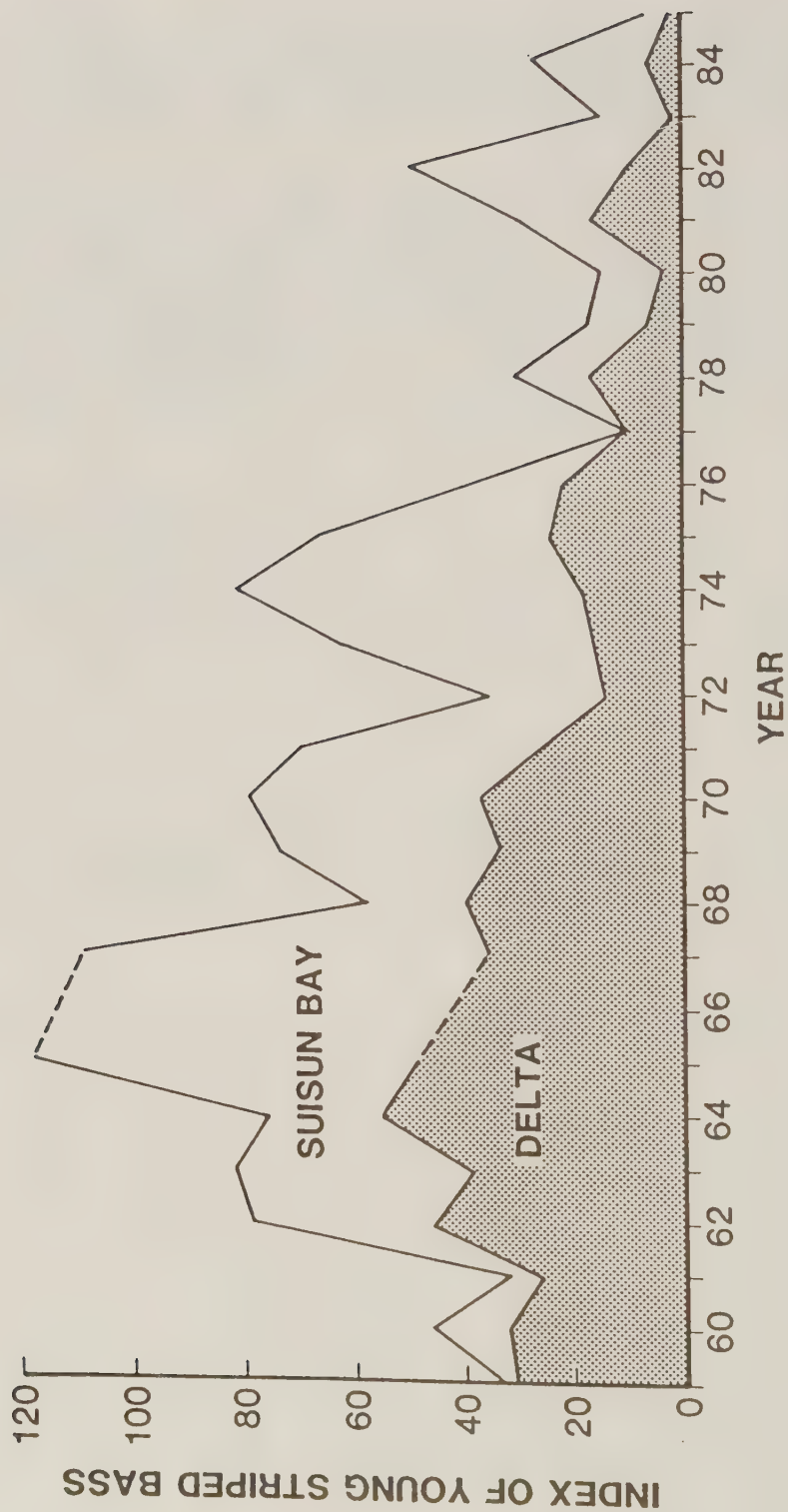


Figure 2A. Decline in the striped bass (*Morone saxatilis*) population in the San Francisco Bay-Delta area (Stevens et al., 1985). Young-of-the-year striped bass (juveniles); change in the index with year. Decline pronounced since 1975.

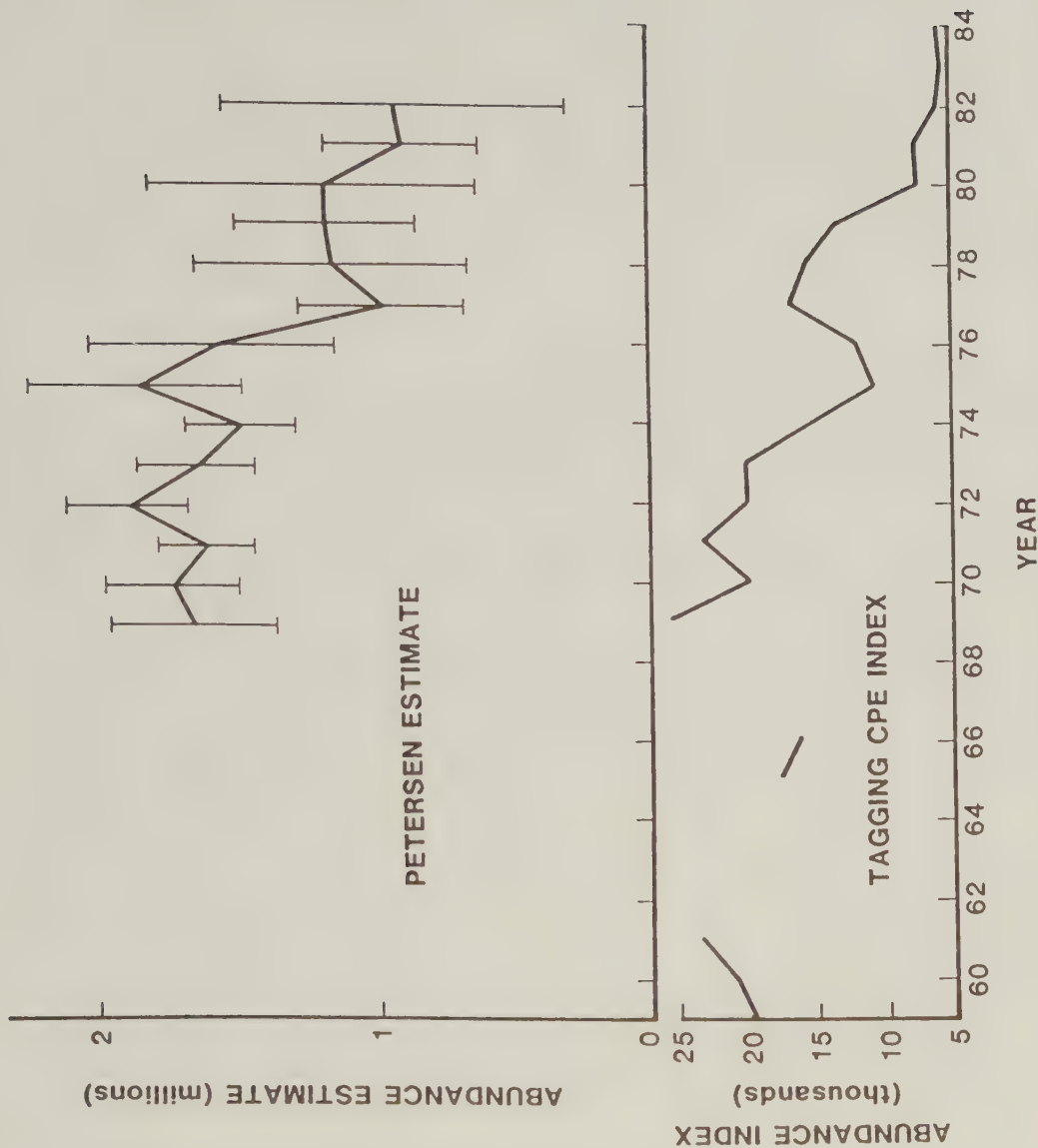


Figure 2B. Two measures of adult striped bass population size; change in Peterson and catch-per-unit effort estimates of adult bass with year. Decline obvious from 1975. (Stevens et.al., 1985)

The interaction of yearly temporal variation in net flow with spatial variation in spawning and nursery habitats appeared to be a major factor in the annual variation in survival of striped bass. We hypothesized that in critically low water years, or when certain pollutant "events", such as spills, occurred during spawning migration, this spatial-temporal equilibrium was disturbed. When this happened, the effects of pollutants and other environmental stress factors appeared to play a larger role in contributing to the mortality of striped bass. This system was thought of as a "model" for the interaction of the anthropogenic stressors of water diversion and pollutants.

To begin research, we derived the following specific goals:

1. To determine the consequences of chronic pollutants impacting a fishery's population.
2. To use striped bass, an apparently declining population in the San Francisco Bay ecosystem, as a "model species" for such a study.
3. To compare the San Francisco Bay-Delta striped bass population to other populations less impacted and more impacted by pollutants.
4. To determine the condition or health of striped bass caught in the field, and if in poor condition, to determine correlation with pollutant burdens in tissues.
5. To do laboratory studies to corroborate field-determined correlations between fish condition and pollutant burdens.
6. To formulate a quantitative model showing relationships between pollutants and the condition of the bass population in terms of reductions in growth, reproduction, and survival.
7. To provide recommendations to appropriate agencies involved with management of fisheries, specifically, the striped bass fishery, and to agencies responsible for the maintenance of water quality and the health of marine ecosystems.
8. To cooperate with other agencies in determining the main sources of pollutants deleteriously affecting striped bass.
9. To cooperate with other agencies in determining the pollutant burdens in striped bass potentially harmful to human health.

10. To cooperate with other agencies in determining the relationship of pollutant effects on striped bass to other ecosystem processes, e.g., water outflow and diversion and other species in the striped bass food chain.
11. To make field tests of predictive models.

The results here are updated from a previous report (Whipple, 1984) and summarized from a manuscript in preparation: "A multivariate approach to studying the interactive effects of inherent and environmental factors, including pollutants, on striped bass in the San Francisco Bay-Delta, California" by Jeannette A. Whipple, R. Bruce MacFarlane, Maxwell B. Eldridge, and Pete E. Benville, Jr.

Methods

We have examined approximately 500 fish captured in the field from the San Francisco Bay-Delta (400); the Coos River, Oregon (41); Lake Mead, Nevada (30); and from the Hudson River, New York (26). Techniques of histopathological examination and autopsy have been developed to assess the health of striped bass and to continue annual monitoring (Whipple, et. al. 1984). Approximately 350 characteristics of the fish were examined initially -- from the biochemical level to organ system and individual organism levels -- to determine the best measures of health. Subsamples were taken of liver, ovaries and muscles to determine burdens for the following major classes of pollutants: petrochemicals or petroleum hydrocarbons (monocyclic aromatics, polycyclic aromatics), chlorinated hydrocarbons (including PCBs, toxaphene, DDT, and its metabolites and others), and heavy metals (copper, iron, zinc, cadmium, mercury, lead, nickel, and others). Tissues were also scanned for EPA's priority pollutants.

Multivariate statistical techniques, including principal component factor analysis (Nie, 1975), were applied to the field data to determine correlations between sets of variables describing conditions and the pollutant burdens. The following summary of results includes correlations and regressions found significant in multiple regression analyses at the $P < .05$ level or less. Several laboratory experiments were performed to verify correlations seen in field fish (Jung, Whipple, and Moser, 1984).

Results and Discussion

The following summary of specific results apply to the goals above:

1. Location. There were differences among locations. The greatest proportion of the variability was attributable to different sampling locations. Thus, factor analyses were separated by location before assessing the other variability.

- o Fish from the San Francisco Bay-Delta estuary were in poorer health or condition than fish from the Coos River, Oregon. A 1982 sample indicated that Hudson River fish were also in better health than those from the San Francisco Bay-Delta.
- o Comparisons with samples from Lake Mead, Nevada showed that fish from Lake Mead were definitely less parasitized and had lower pollutant burdens than those from the San Francisco Bay-Delta system. Lake Mead fish, on the other hand, had poor body condition, indicating starvation and insufficient food.
- o Fish from the San Francisco Bay-Delta had higher tissue concentrations and a greater number of separate petrochemical compounds than did those from the Coos River, Oregon or the Hudson River, N.Y., except for some xylenes, which were relatively high in all populations of fish sampled.
- o Fish from the Coos River had the lowest concentrations of chlorinated hydrocarbons and heavy metals.
- o Fish from the Hudson River had higher concentrations of PCBs in gonads and muscle, and higher concentrations of chlordane and dieldrin in gonads than did San Francisco Bay-Delta fish.
- o Fish from the San Francisco Bay-Delta had higher levels of copper, zinc, cadmium, and nickel in gonads; higher levels of copper, zinc, mercury, and nickel in liver. Hudson River fish had higher levels of mercury in gonads and muscle and higher cadmium in liver.
- o Lesions caused by host reactions to cestode or tapeworm larval parasites (Lacistorhynchus tenuis) were found only from the San Francisco Bay-Delta.

The concentrations of several other types of parasites were also higher in fish from the San Francisco Bay-Delta area than in fish from any other area. Hudson River fish had a totally different parasite assemblage than fish from the West coast.

- o Egg condition in fish from the San Francisco Bay-Delta was significantly poorer than in fish from any other area sampled.
- o Fish from San Joaquin River were in poorer condition than those from the Sacramento River, showing decreased body condition, higher levels of cestode larvae, and higher concentrations of zinc and other metals.

- o Results show that it is difficult to find a "control population" for comparison with the California population because all examined so far have been impacted in some way by pollutants and/or have significant environmental differences. Nevertheless, of all populations examined, the San Francisco Bay/Delta fish appear in the worst health.
2. Sex. Although most fish sampled were females, both sexes were impacted. Because sexes were sampled differently, and because of strong sexual differences, sexes were also separated in the factor analysis.
- o Males had higher levels of petrochemicals and PCBs in the liver and primarily toluene in testes.
 - o Females had higher levels of petrochemicals in ovaries, higher levels of metals in all tissues and higher levels of PCBs in ovaries than males had in testes.
 - o Body and liver condition was poorer in males than in females.
3. Other Factors. After location and sex, a large proportion of the variation (in the selected variable data base) was accounted for by the factors of age, color pattern, sexual maturity, pollutants, year, the time in the prespawning season, and parasites. An example of factor analysis results is given for the San Joaquin River from 1978-1983 Table 1.
- o Year. Concentrations of petrochemicals varied with year (1978 to 1984) of sampling (Table 2). Most separate compounds and higher levels were found in striped bass in 1978, 1979, and 1981. Some fish from all years, however, contained petrochemicals (except small sample of 7 fish in 1982). Cestode larvae and lesions varied yearly and related to age and sexual maturity of adults. Egg condition was poorest in 1978, 1979, and 1981, correlating significantly with petrochemical concentrations in the liver and ovaries.
 - o Age. Older fish were in poorer condition, with reduced fecundity, higher parasites loads, and greater concentrations of some pollutants, particularly PCBs and metals.
 - o Color pattern type. There were different growth and reproduction rates, body proportions, and pollutant and parasite burdens in fish of different color pattern type (e.g. solid-striped, broken-striped, etc.).

Table 1. -- Factor analysis results for prespawning striped bass. Proportion of variance in data base accounted for by different factors, or sets of variables. San Joaquin River prespawning females (n=157 fish); 1978-1983. The names of factors indicate the major controlling variables in factor sets.

FACTOR NO.	FACTOR NAME	PROPORTION OF VARIANCE	
		FACTOR %	ACCUMULATIVE %
1	AGE, WET WEIGHT	10	10
2	COLOR PATTERN-GENERAL	9	19
3	SEXUAL MATURITY	8	27
4	PETROLEUM HYDROCARBONS: (Gonad & Liver-o-Xylene)	7	34
5	YEAR	6	40
6	CHLORINATED HYDROCARBONS: (Gonad & Liver-PCB's)	5	45
7	CHLORINATED HYDROCARBONS: (Gonad & Liver-DDT)	5	50
8	TIME, TEMPERATURE	4	54
9	PARASITES-CESTODE LESIONS	4	58
10	YEAR	3	61
11	METALS:Liver-(LSI)	3	64
12	PETROLEUM HYDROCARBONS: (Gonad-Ethylbenzene, m-Xylene)	3	67
13	SEXUAL MATURITY	3	70
14	PETROLEUM HYDROCARBONS: (Liver-Ethylbenzene, 1,2-Dimethylcyclohexane)	2	72
15	BODY CONDITION	2	74
16	PETROLEUM HYDROCARBONS: (Liver-Benzene, m-Xylene, 1,2-Dimethylcyclohexane)	2	76
INHERENT FACTORS		ENVIRONMENTAL FACTORS	
		UNIDENTIFIED	
		NATURAL FACTORS POLLUTANT FACTORS	
32%		17% 27%	
		24%	

Table 2.-- Year factor; ranked differences among years in inherent characteristics, environmental variables and condition of striped bass. Based on factor analyses of prespawning female striped bass collected from April to June; San Joaquin River. Loadings on factors greater than or equal to 0.30. Ranked from highest (1) to lowest (7) total mean values. NS = not sampled; NM = sampled, but not measured.

YEAR1 (N)	1978 (59)	1979 (42)	1980 (21)	1981 (12)	1982 (7)	1983 (16)	19842 (21)
VARIABLE							
<u>Inherent Factors</u>							
Age	2	4	7	1	3	6	5
Color Pattern (Stripe Breakage)	6 (8.5)	3 (9.9)	1 (10.5)	5 (9.0)	4 (9.1)	2 (10.1)	2 (10.1)
<u>Environmental Factors</u>							
Outflow	4	5	3	5	2	1	?
Diversion	2	1	2	1	3	4	?
Petroleum HC-							
Monocyclic Aromatics:							
Gonad	4	2	5	1	6	3	NM
Liver	3	5	6	1	4	2	6
Petroleum HC-							
Alicyclic hexanes							
Gonad	3	2	5	3	5	1	5
Liver	3	2	5	4	5	1	5
Metals-Gonad							
Copper	1	NS	3	2	NM	NM	NM
Zinc	2	NS	3	1	NM	NM	NM
Metals-Liver							
Copper	NS	NS	3	2	NM	NM	1
Zinc	NS	NS	3	2	NM	NM	1
Cadmium	NS	NS	NS	2	NM	NM	1
Chromium	NS	NS	NS	1	NM	NM	2
Mercury	NS	NS	NS	1	NM	NM	2
Selenium	NS	NS	NS	2	NM	NM	1
Parasites							
Tapeworm Larvae	6	5	2	6	1	4	3
Tapeworm Lesions	4	1	3	2	5	1	4
Tapeworm Rafts	6	1	4	5	6	3	2
Total Parasites3 Severity	2	2	5	4	1	4	3
<u>Condition Factors</u>							
+Egg Resorption	1	2	4	2	6	3	5
(More resorbed eggs and ovaries and abnormalities, less delayed maturation).							

1 Sample sizes in 1981 and 1982 were small because of reduced population size of prespawning adults.

2 Some outflow and diversion data not available.

3 All types of parasites and host reactions.

- o Sexual Maturity. Spent females were significantly different than maturing females in having higher concentrations of petrochemicals in the liver (particularly toluene) and higher parasite burdens. Young prespawning females exhibited more alterations of egg maturation rate and resorption associated with petrochemicals. Young prespawners were also more likely to have open or only partly healed cestode lesions.
 - o Parasites. A significant proportion of adults (approximately 33 percent had scars from cestodes-induced lesions. These fish were in generally poorer condition than those without scars, and had higher levels of pollutants, particularly petrochemicals. Young adults and juveniles showed open lesions from these parasites (Figure 3). Many of the older fish had relatively large numbers of Anasakid roundworm larvae, sometimes in muscle. This worm can impact the health of man.
4. Pollutants. Adult striped bass from the San Francisco Bay-Delta system contained relatively high levels of pollutants from several classes (Table 3. ranges; Whipple, et. al. in prep. contains all means and standard deviations). Some of these pollutants showed strong correlations with poor health and condition, parasite burdens and impaired reproduction.
- o Petrochemicals. There were significant levels of monocyclic aromatic hydrocarbons, including benzene, toluene, ethylbenzene and three isomers of xylene, in tissues of striped bass. There were also significant levels of alicyclic hexanes. All these components are relatively toxic to fish (Benville and Korn, 1977; Benville et. al. 1985). In addition to the effects on the fish associated with these compounds in liver and ovaries, the muscle tissue appeared to differentially accumulate toluene which has been shown previously to cause the "tainting" or bad flavor in other species. Other data (Vassilvos, et. al. 1982) show that there were also relatively high levels of polycyclic aromatics in adult striped bass. For example, levels of thiophenes in fish from the San Francisco Bay-Delta were higher than in fish from other areas. These compounds are carcinogenic.

High levels of petrochemicals in the fish correlated strongly with deleterious effects measured, including egg resorption (Figure 4) and abnormal reproduction. The mean egg resorption by year, comparing locations, is shown in Figure 5. In 1982, sample size (7) was



Figure 3. Lesioned striped bass. Open lesion is a result of fish over-reacting to tapeworm larvae infection, followed by bacterial infection. In older bass, lesions may be healed with only scars showing on the surface.

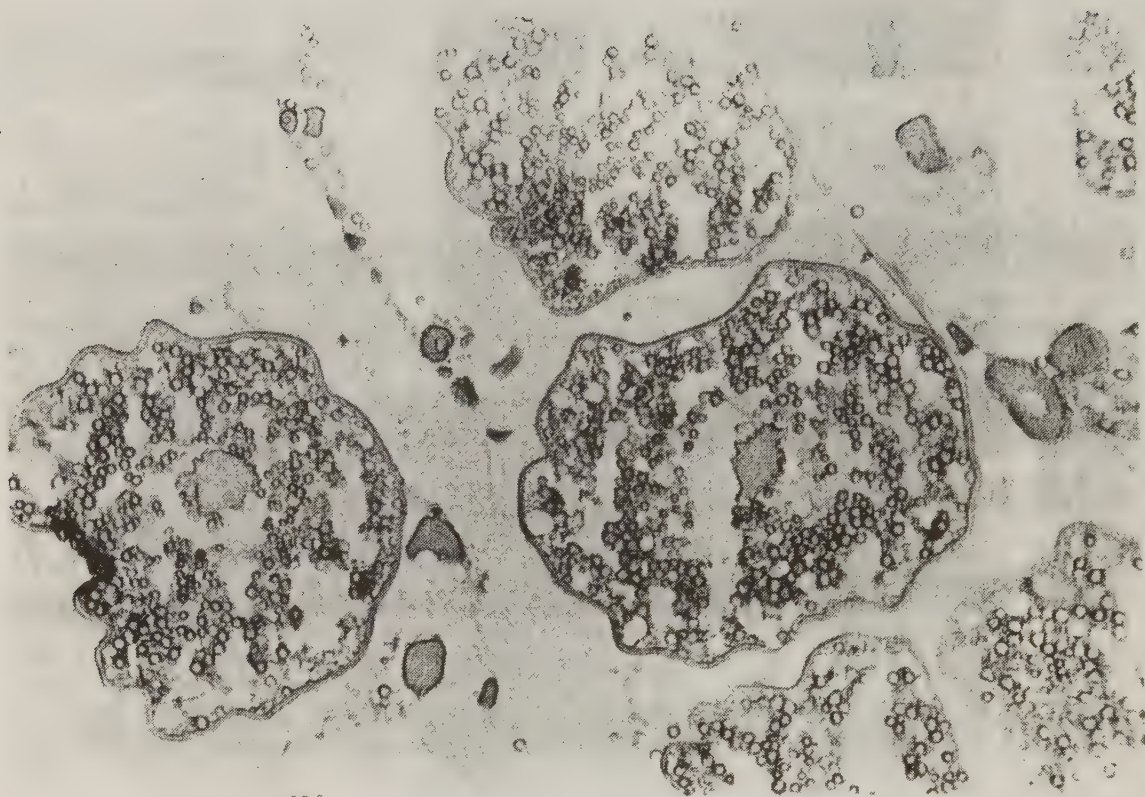


Figure 4A. Eggs from ovaries of striped bass.
Normal eggs in secondary to tertiary yolk stage.

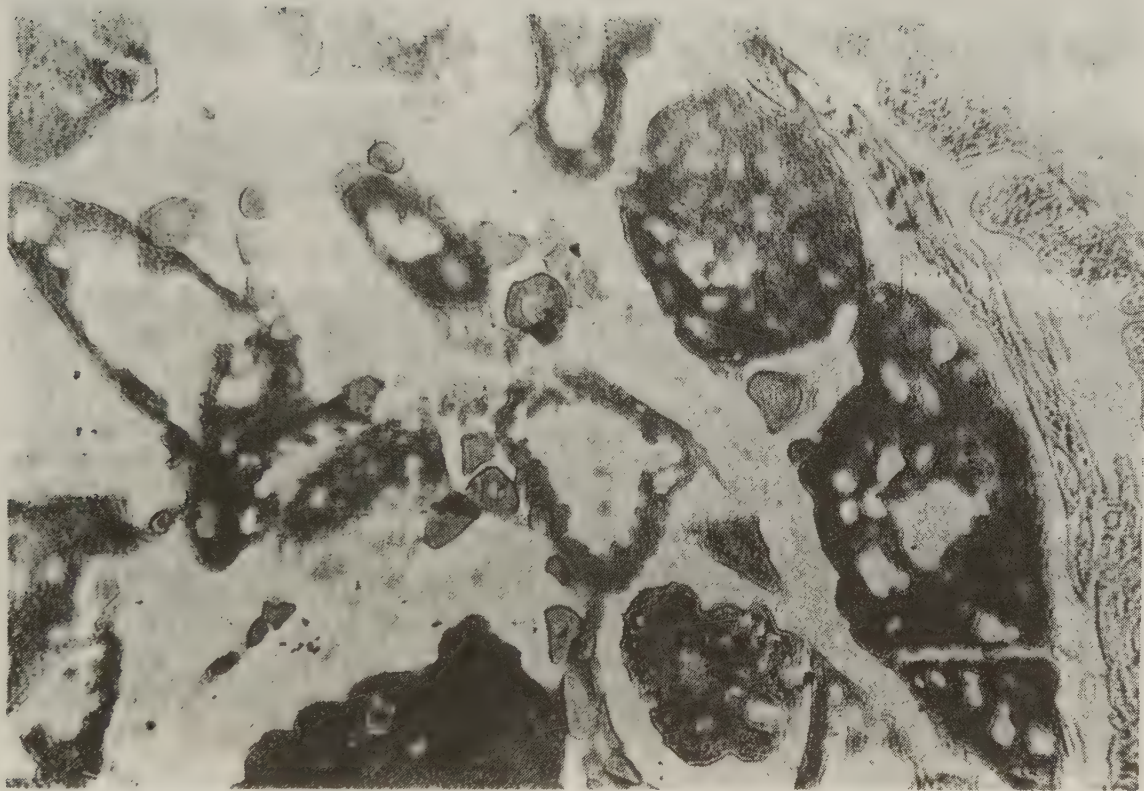


Figure 4B. Abnormal eggs, in varying stages of resorption. This condition is associated with petrochemicals.

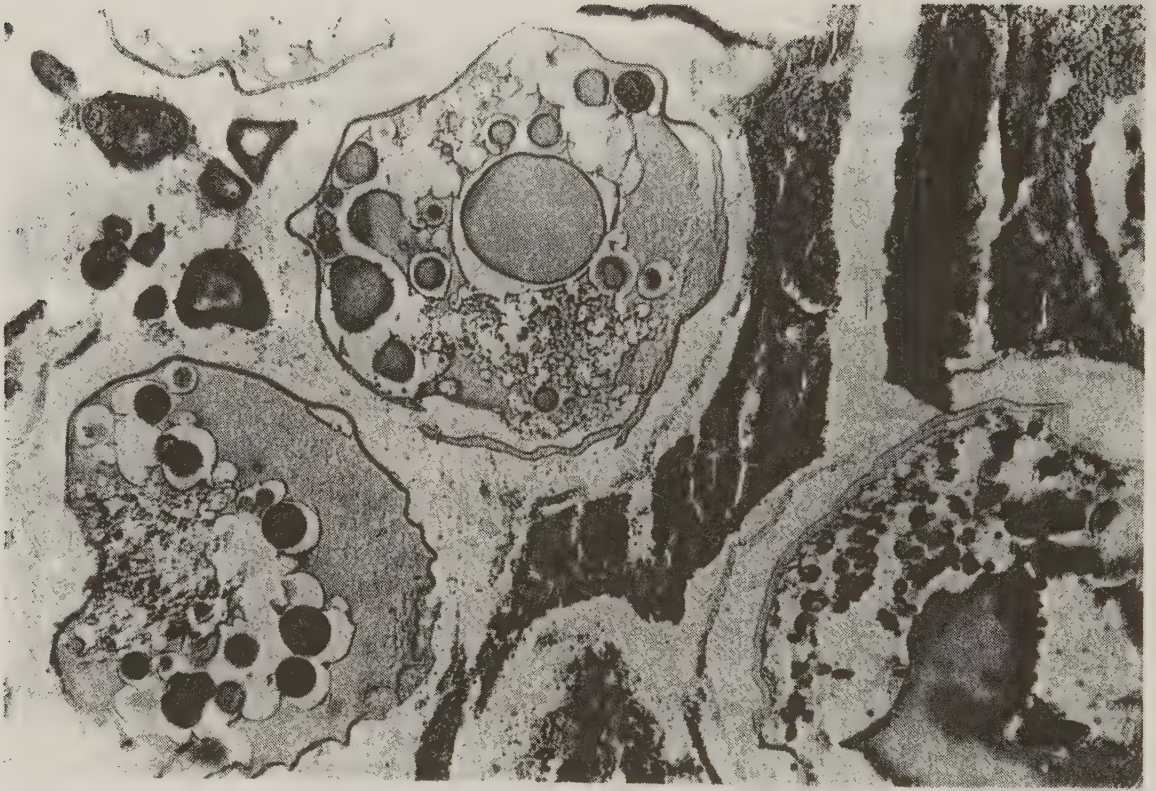


Figure 4C. Abnormal eggs, in late development stage, being resorbed. Note dark areas of melanin-containing melanomacrophages in intercellular areas. This condition is associated with DDT.

REPRODUCTION: PERCENT EGG RESORPTION

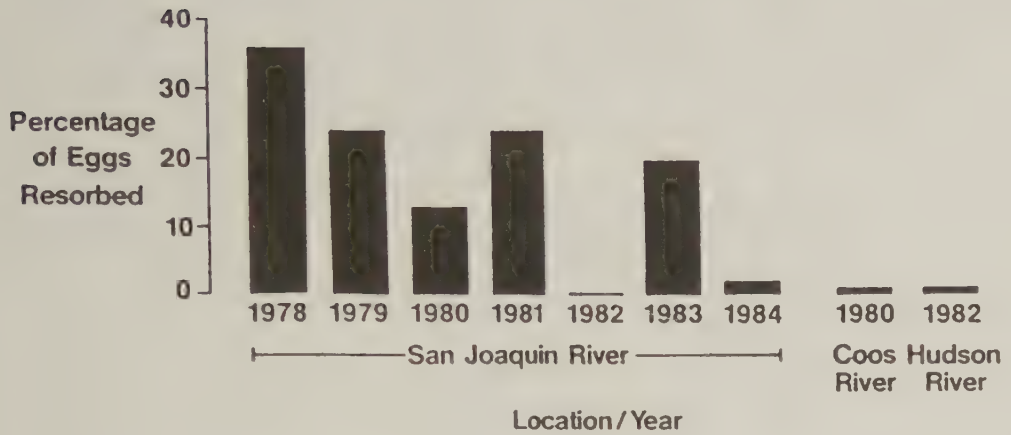


Figure 5. Mean egg resorption in striped bass prespawning females by year (1978-1984) and at different locations.

too small for a representative assessment. An example of the proportion of egg resorption because of various factors, including petrochemicals, is shown in Figure 6. Reduced egg condition was particularly associated with high concentrations of ethylbenzene and 1, 2-dimethylchyclohexane. These components are also among the more toxic and persistent in tissues of the low-boiling point petrochemicals.

High concentrations of benzene were associated with blood cell destruction, abnormal blood cell development and other blood parameters. There was also a correlation between the presence of lesion scars and petrochemical concentration, particularly toluene and ethylbenzene.

Concentrations of monocyclic aromatics in the tissues of field fish correspond to levels reached in tissues of fish exposed in the laboratory to 50-100 ppb monocyclics (particularly benzene). The bioaccumulation was generally about ten times higher than the water concentrations (Whipple, et. al. 1981).

- o Chlorinated hydrocarbons. There were relatively high levels of PCBs, DDT, and its metabolites, and other chlorinated hydrocarbons, including toxaphene, in liver and gonads and fish from the San Francisco Bay-Delta estuary (Table 3). Concentrations of some chlorinated hydrocarbons were at levels resulting in deleterious effects in other fish (Jung, Moser, and Whipple, 1984). The presence of DDT in liver and gonads (not metabolites DDD and DDE) was associated with abnormal egg development and necrosis of eggs (Figure 4C). Delayed egg maturation rates (vitellogenesis) were associated with PCBs in ovaries.
- o Heavy metals. There were relatively high levels of zinc and copper and other metals in adult striped bass livers and gonads (Table 3). The concentration of zinc and other metals correlated with decreased body and liver condition in some fish. Cadmium, nickel, zinc, and copper also correlated with reductions in egg viability in the 1981 San Joaquin River sample. High levels of other metals were found, particularly mercury, in some fish.
- o Pollutant interaction. Initial results show pollutants interacted in affecting the fish. In particular, high levels of petroleum hydrocarbons interacted with chlorinated hydrocarbons to produce effects on reproduction. Data also show that hydrocarbons and metals interact to produce deleterious effects on egg and liver condition.

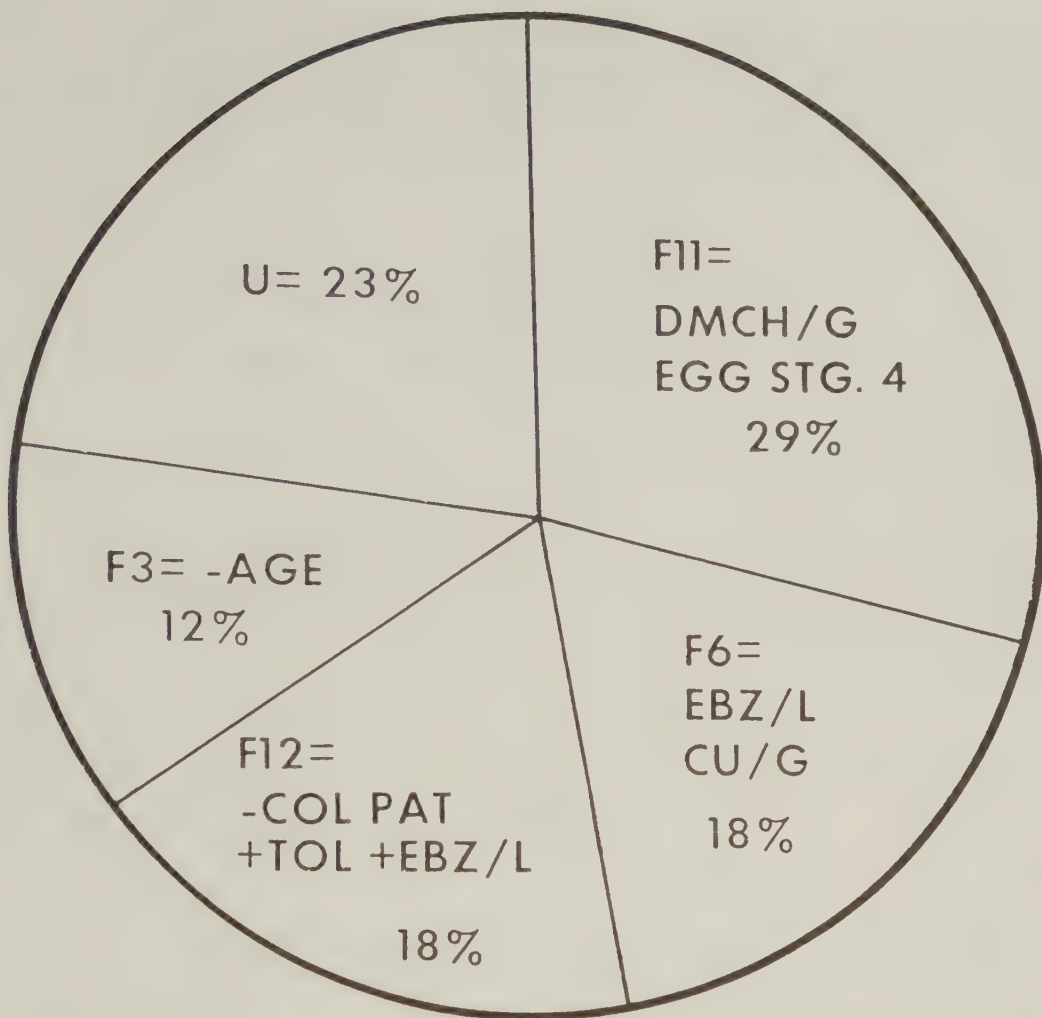


Figure 6. Proportion of total variance in egg condition (egg resorption) accounted for by different factors. Derived from factor equations in factor analysis. Most fish collected in this year had high levels of monocyclic aromatics in the liver and gonads.

EXAMPLE: San Joaquin River; 1978. N=59 females.

$$+EGG \text{ RESORPTION} = .35F3 = .42F6 = .54F11 = .42F13 = U$$

U = Unidentified Variance; DMCH = 1,2,-dimethylcyclohexane;
EGG STG. = Egg Stage; EBZ = Ethylbenzene; CU = Copper;
COL PAT = Color Pattern; TOL = Toluene.

Table 3.—Concentration ranges of selected pollutant classes from the San Francisco Bay-Delta estuary; data available to present. Tissue data from adult prespawning striped bass (*Morone saxatilis*). Tissue concentrations in ug/g (ppm) wet weight hydrocarbons ug/g (ppm) dry weight for metals. Data from this study and Vasillaros et al. (1982), Eaton (1975), and Girvin et al. (1978). ND = not detectable; NM = not measured.

Pollutant class	Concentration in water (dissolved)	Concentration in tissues (ppm)		
	ug/L (ppb)	Liver	Gonads	Muscle ¹
Petroleum hydrocarbons				
Total monocyclic aromatics	1-200	0.01-10	0.01-10	0.01-7.52
Total alicyclic hexanes	ND	0.02-5.0	0.02-10	0
Total polycyclic aromatics (All components)	?	--Whole fish composite 10.0----		
Total naphthalenes (Dicyclics)	?	--Whole fish composite 0.009---		
Total sulfated thiophenes	?	--Whole fish composite 6.0----		
Chlorinated hydrocarbons				
DDT	ND	0.09-0.12	0.10-0.68	NM
DDD	ND	0.10-0.98	0.13-2.8	NM
DDE	ND	0.03-3.1	0.10-12	NM
Toxaphene	0.03-0.32	?	0.20-2.0	NM
Total PCB's	ND	0.25-13	0.81-13	0.20-4.0
Trace metals				
Cadmium	0.08-0.20	0.29-9.4	0.08-0.71	0.18-1.3
Chromium	ND	0.61-3.3	0.51-2.2	0.31-2.2
Copper	1-4	1.0-220	1.0-35	0.10-12
Lead	0.03-0.12	0.09-0.37	0.06-0.89	0.11-0.62
Mercury	ND	0.49-13	0.03-0.96	0.06-1.6
Nickel	1-6	0.60-1.8	0.37-2.1	0.50-2.0
Selenium	?	3.2-21	NM	NM
Zinc	2-6	7.0-250	3.0-310	1.0-66

¹Muscle analyses with no skin attached. Mostly toluene in muscle.

Pollutants most implicated in deleterious effects on fish are, in order: ethylbenzene, 1, 2-dimethylcyclohexane, benzene toluene; DDT, copper, zinc, cadmium, nickel, and mercury. However, other pollutants may be involved that we were unable to measure. For example, recent measurements show that there are relatively high levels of selenium in liver and gonads of striped bass. Several pollutants, particularly chlorinated hydrocarbons, polycyclic aromatics, cadmium, and mercury were found at levels sufficiently high not only to affect the health of the fish but also to potentially affect human health.

The relevant fact is that there are strong associations of these pollutants with decreased condition, growth, reproduction, and possibly survival of striped bass.

5. Laboratory experiments. Experiments performed in the laboratory showed that representative pollutants (benzene and zinc) produced effects similar to those observed in the field (Jung, Whipple, Moser, 1984; Whipple, et. al. ms in prep.). Laboratory exposures equivalent to high chronic water levels in the field resulted in tissue concentrations similar to those in field fish (magnitude of concentration of benzene and/or other total MAH was approximately 10X). The effects on condition of tissues and organs, and other parameters were also similar. The following were some major results:

Adults:

- o Benzene induced egg resorption in prespawning females similar to that in field fish. Fish with higher pollutant burdens when exposed to benzene were most seriously affected.

Juveniles:

- o Uptake of benzene and zinc appeared to be antagonistic -- high concentrations of benzene in the liver were correlated with low concentrations of zinc.
- o Benzene appeared to accelerate and increase the inflammatory response to roundworm larvae.
- o Benzene was correlated with blood cell destruction followed by increased production of immature red and white blood cells.
- o Zinc was correlated with decreased liver condition (LSI).

Zinc was correlated with decreased levels of serum proteins hypothesized to be immunoglobulins.

- o Fish exposed to benzene or zinc had higher levels of protozoan gill parasites than controls.
- o The effects of benzene and zinc together resulted in greater effects on the fish than either pollutant alone, including the following:
 - Inflammatory response to parasitic worms was accelerated.
 - Blood cells and serum proteins were more deleteriously affected.
 - Liver tissue was more deleteriously affected.

6. Population Effects. Although influences other than toxic chemicals (e.g, Delta outflow, larval food supply and entrainment; Stevens et. al. 1985) also are involved in the decline of the striped bass fishery, the following hypotheses were also supported by the study findings.

- o There has been a reduction in numbers of larvae to young-of-the-year juveniles. Laboratory studies showed that larvae accumulate high levels of toxic pollutants (e.g., benzene) with deleterious effects (Eldridge et. al. 1981). These studies should be corroborated in the field. We suggest that toxic pollutants and parasitic cestode lesions may also increase mortality of juveniles and subadults.
- o There has been a reduction in the number of spawning adults. The poorer condition of older adults is at least partially due to the combined effects of parasitism and pollutants. It is also likely that increased mortality of adults has occurred, leading to fewer older fish that normally have the highest fecundity. Ultimately, this will lead to decreased egg production by the population and decreased abundance of juveniles. According to Stevens et. al. (1985), this is probably an important cause of the decline in the striped bass population.
- o The reduction in the number of eggs (fecundity) per spawner, due to the combined effects of pollutants and parasitism, was at least 36-50 percent in 1978. This reduction was assessed from measurements of:
 - delayed rate of maturation (vitellogenesis)

- partial egg resorption
- complete egg resorption in maturing ovary
- no ovarian maturation in sexually mature fish
- egg death
- reduction in number of eggs (fecundity)

Pollutants, therefore, can lead to additional decreases in the egg production of the population. Additional delayed mortality may have occurred in embryos and larvae after spawning, resulting in even further reduction in survival.

- o Multiple regression analyses were done with data collected for the years 1978 to 1984 (7 years) from San Joaquin and Sacramento Rivers. Results showed that survival to young-of-the-year related to age distribution of spawning adults, outflow and diversion, petrochemicals and egg resorption. The best correlation was with egg resorption (Figure 7). The hierarchy of relationships is probably as follows (Figure 8): Environmental factors such as lower outflow are associated with higher petrochemical contamination; higher residues of petrochemicals interact with inherent factors in prespawning adults to affect condition and reproduction. Greater egg resorption occurs and subsequently there is higher larval mortality. Higher mortality of eggs and larvae results in lower abundance of juvenile striped bass. The important result, in terms of fisheries management, is that recruitment to the fishery is reduced. If successful, this method can lead to the forecasting of recruitment several years in advance. Our results so far, however, are for a short period (7 years) and need to be validated by continued monitoring before conclusions can be drawn.

Conclusions

The San Francisco Bay-Delta estuary has been modified in several ways since humans settled this area (Nichols et. al. 1986). Among the most significant of these is the elimination of habitat for fish and other biota through human activities such as filling of wetlands and diversion of water for agriculture. Further degradation of this estuary due to increased diversion of water and increased disposal of toxic wastes is predicted.

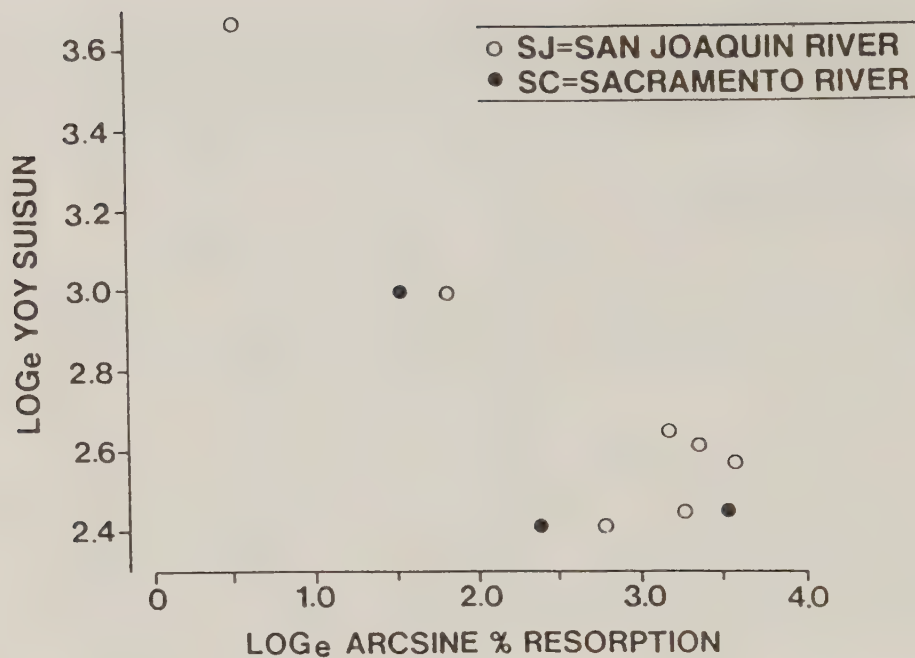


Figure 7. Correlation of yearly mean survival to young-of-the-year juveniles (YOY) with mean egg resorption in adult females of that spawning season. Data on YOY striped bass index from David Kohlhorst

$$\ln \text{YOY Suisun} = 3.60 - .341 \ln \text{Egg Resorption}$$

$$r = -.869; P < .001$$

POPULATION LEVEL EFFECTS

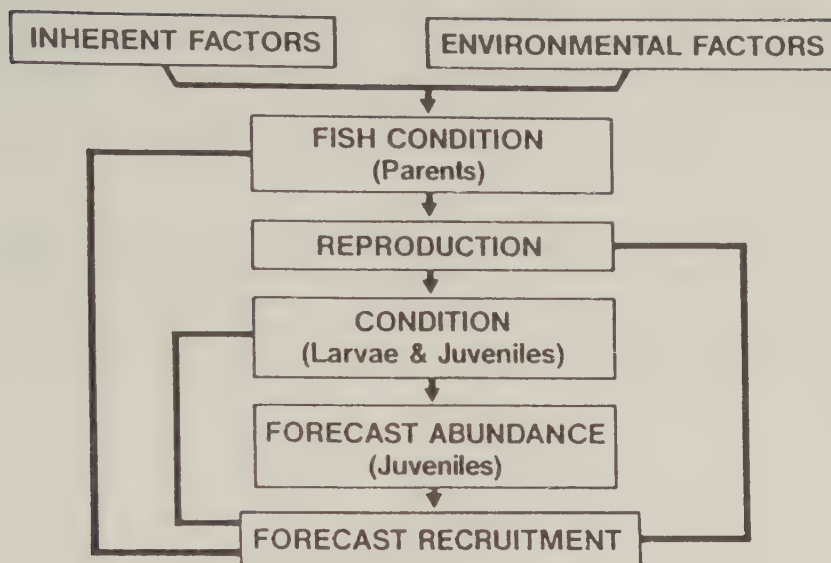


Figure 8. Population level effects. Determining the relationship of environmental factors (e.g. pollutants) on fish condition, reproduction and recruitment to the fishery.

The striped bass population is a major component of the San Francisco Bay-Delta estuary, particularly in past years prior to its decline. It would be of interest to do more research on the relationship of the population dynamics of this species to the flow dynamics of the estuary, and to examine the striped bass in an ecosystem context. This would be of critical importance in making future decisions on water quality and the management of fisheries in the San Francisco Bay-Delta system.

In conclusion, we believe that further investigation of sources and effects of pollutants on striped bass and other biota in the San Francisco Bay-Delta is warranted. We believe also that enough is known for managers and regulators to act now and that any activity reducing the input of these toxic pollutants into the estuary will be beneficial to the health and abundance of the striped bass population.

Acknowledgements

This research was supported by the National Marine Fisheries Service and by a contract from the former Office of Marine Pollution Assessment under the Marine Protection, Research and Sanctuaries Act of 1972 (P.L. 92-532; Title II, Section 202). Further cooperation and support was from the State of California Water Resources Control Board within the Cooperative Striped Bass Study, codirected by Marvin Jung, Consultant. We appreciate the advice, assistance, and cooperation of staff from the CDFG in Stockton, California, particularly Donald Stevens and David Kohlhorst.

References

- Benville, Pete E., Jr. and Korn, Sid, 1977: The acute toxicity of six monocyclic aromatic crude oil components to striped bass (Morone saxatilis) and bay shrimp (Crangon francoscorum). Calif. Fish and Game 63(4):204-209.
- Benville, Pete E. Jr.; Whipple, Jeannette A.; and Eldridge, Maxwell B., 1985: Acute toxicity of seven alicyclic hexanes to striped bass Morone saxatilis and bay shrimp Crangon francoscorum, in seawater. Calif. Fish and Game 71(3):132-140.
- Eaton, Andrew, 1979: Observations on the geochemistry of soluble copper, iron, nickel, and zinc in the San Francisco Bay estuary. Environ. Sci. and Tech. Res. 13(4):425-431.
- Eldridge, Maxwell B.; Benville, Pete; and Whipple, Jeannette A., 1981: Physiologic responses of striped bass (Morone saxatilis) embryos and larvae to low sublethal concentrations of the aromatic hydrocarbons benzene. Proc. Gulf Caribb. Fish Inst. 33:52-68.

- Girvin, Donald C.; Hodgson, Alfred T.; Tatro, Mark E.; and Anaclerio, Roy N. Jr., 1978: Spatial and seasonal variations of silver, cadmium, copper, nickel, lead, and zinc in south San Francisco Bay waters during two consecutive drought years. Energy and Environ. Div., Lawrence-Berkeley Laboratory, University of California, Berkely, CA. Final Report UCID-8008.
- MacFarlane, R. Bruce and Whipple, Jeannette A., 1984: Striped Bass Health Index. In-House report submitted to Advisory Committee for Aquatic Habitat Program, State Water Resources Control Board. April, 1984.
- Moser, Mike; Love, Milton; and Sakanari, Judy A., 1984: Common parasites of California fish. Calif. Dep. Fish and Game, 20 p.
- Moser, Mike; Sakanari, Judy A.; Wellings, Sefton; and Lindstrom, Kris, 1984: Incompatibility between San Francisco striped bass, Morone saxatilis (Walbaum), and the metacestode, Lacistorhynchus tenuis (Beneden 1858). J. Fish Dis. 7:397-400.
- Moser, Mike; Sakanari, Judy A.; Reilly, Carol A.; and Whipple, Jeannette, 1985: Prevalence, intensity, longevity, and persistence of Anasakis sp. larvae and Lacistorhynchus tenuis metacestodes in San Francisco striped bass. NOAA Tech. Rpt. NMFS 29: 4 p.
- Nichols, Frederick H.; Cloern, James E.; Luoma, Samuel N.; and Peterson, David., 1986: The modification of an estuary. Science. 231:567-573.
- Nie, Norman H.; Hull, Hadlai; Jenkins, Jean G; Steinbrenner, Karin; and Bent, Dale H., 1975: SPSS: Statistical Package for the Social Sciences, second edition. McGraw-Hill, N.Y. 675 p.
- Stevens, Donald E.; Kohlhorst, David W.; Miller, Lee W.; and Kelly, D.W., 1985: The decline of striped bass in the Sacramento-San Joaquin estuary, California. Trans. Am. Fish. Soc. 114:12-30.
- Vassilaros, D.L.; Eastwood, D.A.; West, W.R.; Booth, G.M.; and M.L. Lee, 1982: Determination and bioconcentration of polycyclic aromatic sulfur in heterocycles in aquatic biota. In M. Cooke, A.J. Dennis, G.L. Fisher (editors). Sixth international symposium for polynuclear aromatic hydrocarbons: Physical and biological chemistry, p. 845-857. Battelle Press, Columbus, Ohio.

- Whipple, Jeannette A.; Eldridge, Maxwell B.; Benville, Pete, Jr., 1981: An ecological perspective of the effects of monocyclic aromatic hydrocarbons on fishes. In F.J. Vernberg (editors), Biological Monitoring of Marine Pollutants, p. 483-551. Academic Press, N.Y.
- Whipple, Jeannette A. 1982: The impact of estuarine degradation and chronic pollution on populations of anadromous striped bass (Morone saxatilis) in San Francisco Bay-Delta, California. Annual research report submitted to NOAA, OMPA. May 15, 1982.
- Whipple, Jeannette A. 1984: The impact of estuarine degradation and chronic pollution on populations of anadromous striped bass (Morone saxatilis) in San Francisco Bay-Delta, California. A summary for managers and regulators. NOAA, NMFS, SWFC Admin. Rpt. T-84-01, 41 p.
- Whipple, Jeannette A.; Bowers, Michael; Jarvis, Brian; and Moreland, Sharon, 1983: Report on the condition and health of May 1982 sample of Hudson River adult, pre-spawning striped bass. In-house report, NMFS, Tiburon Laboratory. 23 p. (Manuscript in preparation for publication).
- Whipple, Jeannette A.; Jung, Marvin; MacFarlane, R. Bruce; and Fischer, Rahel, 1984: Histopathological manual for monitoring health of striped bass in relation to pollutant burdens. Tech. Mem. NOAA-TM-NMFS-SWFC-46, 81 p.
- Cooperative Striped Bass Study (COBS) Reports:
- Jung, Marvin and Bowes, Gerald, 1980: First progress report on the Cooperative Striped Bass Study (COBS). Calif. State Water Resour. Control Board. Sacramento, CA., 64 p.
- Jung, Marvin, Whipple, Jeannette A., and Moser, L. Michael, 1984: Summary report of the Cooperative Striped Bass Study (COSBS). A study of the effects of pollutants on the San Francisco Bay-Delta striped bass fishery. Draft summary report submitted to the California State Water Resources Control Board.
- Whipple, Jeannette A. and Jung, Marvin, 1981: Cooperative Striped Bass Study (COBS). Appendix I: Procedures for histopathological examinations, autopsies and subsampling of striped bass. Calif. State Water Resour. Control Board, Sacramento, CA., 46 p.
- Whipple, Jeannette A.; Crosby, Donald G.; and Jung, Marvin, 1983: Third progress report: Cooperative Striped Bass Study (COBS). Calif. State Water Resour. Control Board, Sacramento, CA., 208 p.

Comparison of the fatty acid component in structural lipids from dolphins, zebra and giraffe: possible evolutionary implications

G. WILLIAMS, M. A. CRAWFORD

Nuffield Laboratories of Comparative Medicine, Institute of Zoology, Zoological Society of London,
Regent's Park, London NW1 4RY, UK

AND W. F. PERRIN

Southwest Fisheries Marine Center, National Marine Fisheries Service, NOAA, La Jolla,
California, 92037, USA

(Accepted 13 March 1987)

Essential fatty acid compositional data on the structural lipids of mammals which predominantly eat n-3 fatty acids suggests preferential incorporation of n-6 essential fatty acids.

The structural lipids of liver, muscle and brain of five species of dolphin (*Tursiops truncatus*, *Stenella attenuata*, *Steno bredanensis*, *Delphinus delphis* and *Lagenorhynchus obliquidens*), obtained from the wild, contained substantial amounts of arachidonic acid and other n-6 long chain derivatives of linoleic acid. The n-6 to n-3 ratio was approximately 1:1.

Data for two species of leaf-eating land mammals, the zebra, *Equus burchelli* Gray and giraffe, *Giraffa camelopardalis* L., indicate that tissue phosphoglycerides were dominated by n-6 fatty acids.

Contents

	Page
Introduction	673
Methods	674
Source of animals	674
Lipid extraction and fatty acid analysis	675
Results	675
Dolphin lipids	675
Comparative data from zebra and giraffe	676
Discussion	679
References	682

Introduction

Studies on the evolutionary variation of amino acid sequences in proteins have shown that it is largely confined to minor alterations of one or, at the most, a few codons (Nolan & Margolaish, 1968), and the variability in terms of the component proportions of essential amino acids has been found to be small (Crawford, Gale, Somers & Hansen, 1970). Cell structural lipids, with the exception of the brain, exhibit wide variations in the essential fatty acid (EFA) component of cell structural lipids in such a manner that a contribution to evolutionary differences has been suggested (Crawford & Sinclair, 1972; Crawford, Casperd & Sinclair, 1976). There are particularly wide differences in the fatty acids in membrane lipids of marine compared to land animals.

The marine food chain commences with the photosynthetic phytoplankton, having an n-6:n-3 ratio of approximately 1:6 (Ackman, 1982). It progresses through the zooplankton to the fish with

the proportions of the long chain, more unsaturated members of the n-3 fatty acids increasing and resulting in substantial amounts of eicosapentaenoic (C20:5, n-3) and docosahexaenoic (C22:6, n-3) acids becoming available to the dolphins. The fish which have been studied have been found to have an n-6:n-3 balance of between 1:20 to 1:50 (Ackman, Eaton & Jangaard, 1965; Ackman, 1982), and have an essential requirement for n-3 but not n-6 fatty acids for reproduction and growth (Nicolaidis & Woodall, 1962; Cowey, 1976; Fujii & Yone, 1976; Yu & Sinnhuber, 1979).

We previously reported surprisingly large amounts of n-6 fatty acids in the tissues of two bottlenose dolphins (*T. truncatus*) which died in captivity, but could not know if this was natural or pathological (Williams, Davidson, Stevens & Crawford, 1977; Williams, 1981). Similarly, we had observed substantial amounts of linoleic (18:2, n-6) acid in the ethanolamine phosphoglyceride (EPG) from a zebra liver previously obtained from Karamoja, Uganda (Crawford *et al.*, 1976). The zebra is a grass-(n-3 rich)-eating animal. This evidence suggests that a powerful selection mechanism might be operating in the process of cell membrane construction in favour of the n-6 fatty acids in these mammals.

The terrestrial food chain, similar to the marine system, starts with photosynthesis in green leaves, in which the n-3 fatty acids dominate, mainly represented by the parent alpha-linolenic acid (18:3, n-3) (Hitchcock & Nichols, 1971). However, the largest concentrations of plant lipid are found stored in seeds which provide mainly linoleic acid (18:2, n-6). Land mammals have a nutritional requirement for n-6 essential fatty acids both for structural lipid and prostaglandin synthesis (Burr & Burr, 1930; Fiennes, Sinclair & Crawford, 1973; Holman, 1977; Crawford, 1983). In a study of 32 land mammals, the balance between the n-6 and n-3 fatty acids was found to be between 3:1 and 6:1 (Crawford *et al.*, 1976).

Evidence indicates that the Cetacea evolved on land and migrated to the marine environment (Gingerich, Wells, Russell & Ibrahim Shah, 1983). Marine lipids are generally considered to be rich in n-3 essential fatty acids. However, the land food chain is thought of as an n-6 rich source due to the high oil and linoleic acid content of seeds and the dominance of n-6 fatty acids in tissues of land mammals (Crawford *et al.*, 1976). The differential availabilities of n-6 and n-3 fatty acids in land and marine plants offers an interesting opportunity to establish whether the dolphins have developed a marine type nutritional system like that of the fishes or have retained a dependence on the land-based chemistry of their ancestors.

Published data on adipose fat from the fin whale, *Balaenoptera physalus*, (Ackman *et al.*, 1965) reflected its n-3 rich dietary fatty acids; however, the adipose fat would be expected to have a different fatty acid composition compared to the lipids of active tissues. We have taken the opportunity of comparing several species of dolphins with two land-based mammals which similarly eat an n-3 rich diet, the zebra (*E. burchelli* G.) which is a monogastric grazer and the giraffe (*G. camelopardalis* L.) representing the ruminant browsers.

Methods

Source of animals

Dolphin samples obtained from the Southwest Fisheries Center, California, were killed incident to tuna-seining in the Eastern Tropical Pacific (ETP). Five species of dolphin (*Tursiops truncatus*, *Stenella attenuata*, *Steno bredanensis*, *Delphinus delphis* and *Lagenorhynchus obliquidens*) were obtained from the wild in this manner.

The animals were chilled immediately after death and the organs stored at -20°C until analysed. Two animals, one *T. truncatus* and one *L. obliquidens*, were the result of voluntary beaching; these animals were collected and frozen as quickly as possible. The adipose tissue, liver and muscle lipids of 14 dolphins from the 5 species and 2 brains from freshly caught dolphins (*T. truncatus*) were analysed for their fatty acid content. Although the habitats and the diets between the species will be different, for the purpose of this communication we have grouped the data from the 5 species. The individual species data will be the subject of a separate paper to be published elsewhere.

The liver, muscle and stomach contents from the zebra and giraffe were obtained from Karamoja, Uganda through the collaboration of the Uganda Game Department, Entebbe and Makerere University College, Kampala, as described previously (Crawford *et al.*, 1976). Tissues were excised within as short a time as possible after death during a cropping programme; this usually meant within 2–3 minutes. The tissues were frozen in dry ice and thereafter kept at -15°C until being flown to London packed in dry ice. Because the results suggest a general n-6 selection principle, we have reported information on the capuchins (*Cebus capuchin*) which have been studied (Fiennes, Sinclair & Crawford, 1973). Recent data from the koala (*Phascolarctos cinereus*) and the grey kangaroo (*Macropus giganteus*) from eastern Australia (Naughton, 1981) have also been included (Table V).

Lipid extraction and fatty acid analysis

Total lipids were extracted from the tissues by the method of Folch, Lees & Stanley (1957). After solvent extraction (chloroform/methanol), the phosphoglycerides were separated from the tissue lipids and triglycerides from adipose tissue by thin-layer chromatography (TLC). Identification was made by developing alongside, known standards (Sigma Chemical Co. Ltd., Poole, Dorset, UK) using methods described previously (Sinclair, 1975). The fatty acids from the individual phosphoglyceride and triglyceride fractions were converted to methyl esters by transmethylation and determined by gas liquid chromatography as previously described (Sinclair & Crawford, 1972). Quantitation of the individual fatty acids was accomplished using an Infotronics 308 automatic digital integrator. A Pye Unicam series 104 gas chromatograph equipped with dual flame ionization detectors was used throughout. The column (1.5 M $\times$ 7 mm I.D.) was packed with 10% polyethylene-glycol adipate on Chromosorb W (60–70 mesh). The oven temperature was maintained at 190°C and the carrier gas (nitrogen) flow was 40 ml per minute.

Results

Dolphin lipids

The dolphin results are expressed as a weight percentage of the total fatty acids with a chain length from C14–C22 carbons to facilitate comparison with the published data on land mammals. The skeletal muscle cholinephosphoglyceride (CPG) fatty acids of 14 dolphins are represented as the mean and standard error of the mean (SEM) (Table I). The mean and the SEM of the liver CPG fatty acids are also reported (Table II).

The fatty acid analysis of 14 wild dolphins confirmed our observations on captive *Tursiops truncatus* (Williams *et al.*, 1977) that a high proportion of n-6 fatty acids is natural to these marine mammals. The level of arachidonic acid (20:4, n-6) was found to be higher in the tissues of wild dolphins than in comparable tissue of dolphins which had died in captivity. The liver and muscle phosphoglycerides were especially rich in arachidonic acid and there were also significant amounts of the docosatetraenoic acid (22:4, n-6) in the ethanolamine phosphoglycerides (EPG).

TABLE I

Mean (weight %) plus or minus standard error (S.E.) of the fatty acids from skeletal muscle CPG from 14 wild dolphins of mixed species, EPG from two *Tursiops truncatus* and adipose tissue triglyceride TG fatty acids from three *T. truncatus*

Fatty acid	CPG n = 14		EPG n = 2	TG n = 3
	mean	S.E.		
14:0	0.69	0.18	0.36	6.9
16:0	15.8	1.33	6.55	11.4
18:0	12.5	1.33	19.5	1.4
14:1	0.26	0.06	0.09	—
16:1	1.79	0.56	0.98	14.7
18:1	21.7	1.17	16.1	24.7
22:1	0.21	0.1	0.25	10.9
18:2, n-6	1.17	0.13	0.23	0.5
20:3, n-6	0.4	0.15	0.14	0.3
20:4, n-6	14.2	1.1	12.8	0.6
22:4, n-6	0.88	0.9	1.55	0.3
22:5, n-6	0.43	0.1	0.26	0.4
18:3, n-3	0.3	0.12	0.32	0.7
20:4, n-3	0.2	0.06	0.19	—
20:5, n-3	6.4	0.9	2.92	2.2
22:5, n-3	1.2	0.12	1.25	1.8
22:6, n-3	7.6	0.6	8.84	9.2
Tot. sat.	30.3	1.9	26	20.0
Tot. mono.	29.5	2.1	18	50.3
Tot. PUFA	34.8	2.3	29	17.0
Tot. n-3	16.3	1.6	13	13.2
Tot. n-6	18.6	1.2	15	2.1
n-6:n-3	1.14	0.1	1.1	0.16
P/S ratio	1.1	0.1	1.1	0.9

The n-6:n-3 ratio in the tissues of dolphins was found to be about 1:1 to 2:1, which is closer to the ratio found in the tissues of land mammals than that reported for fish. Arachidonic acid (20:4, n-6) was quantitatively the most important of the n-6 fatty acids in the dolphins' tissue. The mean value for liver cholinephosphoglyceride linoleic acid (18:2, n-6) for the 14 wild animals was 1.2%.

Comparative data from zebra and giraffe

The previous data which we published on a variety of land animal lipids described the ethanolamine phosphoglyceride fatty acids. The data on the choline phosphoglycerides indicated that they generally held high proportions of linoleic but relatively lower amounts of arachidonic acid by comparison with the ethanolamine phosphoglycerides (Crawford *et al.*, 1976). In this respect, the differences between the two phosphoglyceride fractions were not especially marked in the zebra but were in the giraffe (Tables III and IV).

Tables III and IV present data from adipose tissue, liver, muscle and brain of two species of land mammals for comparison. Only the data for the main essential fatty acids are represented as these

TABLE II

Mean (weight %) plus or minus standard error (S.E.) from liver tissue CPG from 14 wild dolphins of mixed species and EPG from four *T. truncatus*

Fatty acid	CPG		EPG
	(n=14)	S.E.	(n=4)
16:0	18.0	1.1	5.2
18:0	22.9	1.2	29.7
16:1	3.3	0.6	1.88
18:1	20.0	1.0	14.5
22:1	0.1	0.01	0.2
24:1	0.3	0.01	0.4
18:2, n-6	1.2	0.13	0.94
20:3, n-6	0.6	0.07	0.54
20:4, n-6	10.6	1.2	16.8
22:4, n-6	2.1	0.4	2.6
22:5, n-6	0.85	0.1	0.9
18:3, n-3	0.8	0.3	0.22
20:5, n-3	2.9	0.3	3.67
22:5, n-3	1.4	0.2	3.55
22:6, n-3	5.4	0.9	11.2
Tot. sat.	46.4	1.8	35
Tot. mono.	26.4	0.8	17
PUFA	23.7	2.1	40
Tot. n-3	10.7	1.2	19
Tot. n-6	15.4	1.3	22
n-6:n-3	1.4	0.1	1.2
P/S ratio	0.5	0.1	1.1

illustrate the principal points. As with the dolphins, the adipose tissue fatty acids bore little resemblance to that found in the cell membrane phosphoglycerides. Zebra adipose tissue had an n-6:n-3 ratio in favour of the n-3 fatty acids (1:5.8), but the cell membrane fatty acids were in favour of the n-6 family. The zebra phosphoglycerides contained the highest levels of linoleic acid so far recorded (Crawford *et al.*, 1976). The intake of large amounts of n-3 fatty acids in the diet, and the reflection of this in the adipose tissue of the zebra, bore no significance to the level of this essential fatty acid in the structural lipids.

The giraffe was selected as a ruminant in which a high proportion of the dietary essential fatty acids would be hydrogenated in the rumen. This was reflected in a low content of n-6 essential fatty acids in the adipose tissue but substantial amounts in the structural lipids.

Because of the extreme contrast of the dolphins' dietary lipids, one might have expected any significant response of mammalian brain lipids to diet to be observed in this species; however, this was not the case. Despite the differences in adipose and liver fatty acids in the species described, the composition of the brain choline and ethanolamine phosphoglycerides of the different species was similar (Table IV). Although large proportions of linoleic acid was detected in the liver phosphoglycerides of the zebra, there was little of this essential fatty acid in the brain. In the giraffe and the dolphin, the profile was similar, with arachidonic acid (20:4, n-6) and docosatetraenoic acid (22:4, n-6) being the principal metabolites of linoleic acid (18:2, n-6) and docosahexaenoic acid (22:6, n-3) being the main derivative of alpha-linolenic acid (18:3, n-3).

TABLE IIIa

Mean (weight %) plus or minus standard error (S.E.) of the essential fatty acids from liver CPG and EPG and adipose tissue from two large land mammals, zebra (*Equus burchelli*) and giraffe (*Giraffa camelopardalis*)

	Zebra			Giraffe		
	Liver CPG	EPG	Adipose tissue	Liver CPG	EPG	Adipose tissue
18:2, n-6	42.2 (2.9)	31.6 (3.0)	7.88 (3.0)	25.4 (2.5)	9.69 (3.3)	3.67 (0.5)
20:2, n-6	0.22 (0.05)	0.10 (0.06)	0.04 (0.01)	0.36 (0.09)	0.28 (0.05)	0.20 (0.02)
20:3, n-6	0.63 (0.09)	0.29 (0.08)	0.11 (0.01)	0.89 (0.09)	0.30 (0.04)	0.10 (0.06)
20:4, n-6	4.10 (0.11)	4.83 (0.09)	0.02 (0.08)	8.33 (0.10)	14.2 (0.22)	0.11 (0.03)
22:4, n-6	0.12 (0.05)	0.22 (0.05)	—	0.86 (0.04)	2.12 (0.03)	—
22:5, n-6	0.02 (0.01)	0.06 (0.02)	—	0.22 (0.06)	1.19 (0.09)	—
Total n-6	47.3	37.1	8.0	36.1	27.8	4.1
18:3, n-3	3.44 (0.87)	1.65 (0.25)	47.5 (5.22)	3.70 (0.55)	2.11 (0.31)	2.30 (0.19)
20:5, n-3	0.33 (0.01)	0.82 (0.03)	0.03 (0.01)	0.44 (0.05)	0.12 (0.03)	0.02 (0.01)
22:5, n-3	1.22 (0.20)	2.21 (0.24)	—	1.82 (0.94)	9.34 (0.75)	—
22:6, n-3	0.34 (0.04)	0.46 (0.06)	—	0.35 (0.04)	1.45 (0.08)	—
Total n-3	5.33	5.14	47.5	6.31	13.0	2.32
Ratio n-6:n-3	8.9	7.2	0.17	5.7	2.1	1.8

Data on the chemical composition of East African grasses and browse materials have been published (Dougall, Drysdale & Glover, 1964). There are few published data on the lipid chemistry of these plants and such a study would be a substantial undertaking. To obtain an index of average food intakes, the stomach contents were analysed from the giraffe and the zebra. It should be accepted that these data only refer to single time points. The animals were obtained in December and in June, examples of the dry and the end of the rainy season. There was approximately 35% more linoleic acid (18:2, n-6) in the stomach contents of three zebra taken in the dry season compared to three zebra in the wet season but the sample numbers were too small for a statistical comparison. For the purpose of this analysis, the data have been pooled.

Preliminary analysis of lipids from plants commonly eaten by zebra and giraffe indicate that the leaf and seed material of the plants studied had the expected composition. The seeds from the *Acacia* (*Acacia sinagalensis*) varieties contained significant amounts (5–18%) of alpha-linolenic acid (18:3, n-3), whilst the balenites (*Balenites aegyptiaca*), which has a very hard protective shell, had a high proportion (70%) of its fatty acids as linoleic acid and only 0.2% alpha-linolenic acid. Examination of the stomach contents of giraffe demonstrated that approximately one-third of the balenite kernels were broken open, presumably by mastication, but the remainder were intact and would have passed through the animal.

TABLE IIIb

Mean (weight %) plus or minus standard error (S.E.) of the essential fatty acids from muscle CPG and EPG from two large land mammals, zebra (*Equus burchelli*) and giraffe (*Giraffa camelopardalis*)

	Zebra		Giraffe	
	CPG	EPG	CPG	EPG
18:2, n-6	40.2 (3.6)	31.6 (3.4)	24.4 (2.1)	11.3 (1.8)
20:2, n-6	0.42 (0.06)	0.22 (0.02)	0.31 (0.04)	0.11 (0.03)
20:3, n-6	2.14 (0.15)	1.90 (0.16)	2.66 (0.23)	1.30 (0.22)
20:4, n-6	3.00 (0.40)	4.51 (0.39)	7.41 (0.85)	12.8 (1.05)
22:4, n-6	0.10 (0.02)	1.10 (0.08)	0.55 (0.03)	3.84 (0.18)
22:5, n-6	0.02 (0.01)	0.27 (0.03)	0.32 (0.04)	1.24 (0.11)
Total n-6	45.9	39.6	35.6	30.6
18:3, n-3	3.67 (0.65)	2.88 (0.27)	3.45 (0.35)	2.74 (0.30)
20:5, n-3	1.54 (0.20)	1.32 (0.09)	1.39 (0.14)	0.75 (0.04)
22:5, n-3	1.20 (0.22)	2.25 (0.21)	4.52 (0.51)	7.84 (0.66)
22:6, n-3	0.23 (0.02)	0.58 (0.03)	0.25 (0.02)	1.26 (0.02)
Total n-3	6.64	7.03	9.61	12.6
Ratio n-6:n-3	6.91	5.6	3.7	2.4

Discussion

The data demonstrate that, despite the high proportion of n-3 fatty acids in the marine environment, the free-living dolphins have remarkably high concentrations of arachidonic and other n-6 fatty acids in their tissue or membrane phosphoglycerides. In this respect, they are similar to land mammals, where the balance between the n-6 and n-3 families of fatty acids in membrane systems (Crawford *et al.*, 1976) is distinctly different from that of fish (Ackman, 1982). The high proportion of arachidonic acid is of particular interest as it is a principle precursor for the n-6 series of eicosanoids synthesized by land mammals.

The high levels of arachidonic acid and other long chain n-6 fatty acids in wild-caught dolphins raises the question as to their source. The sea-weed, *Chrondrus crispis*, contains 24% arachidonic acid (Ackman, 1982) and Sargent (1976) has reported at least one phytoplankton to contain similarly high proportions of arachidonic acid which, when consumed by the zooplankton, would enter the food chain. Squid and perhaps other cephalopods could provide significant amounts of arachidonic acid as they have been estimated to represent about 30% of the diet of some species of dolphin in the wild (Fitch & Brownell, 1968). Lilly & Bottino (1981) have identified and characterized arachidonic acid in the muscle and organs of the Gulf of Mexico shrimp (*Penaeus*

TABLE IV

Mean (weight %) plus or minus standard error (S.E.) of the essential fatty acids from zebra ($n=6$) (*Equus burchelli*) and giraffe (*Giraffa camelopardalis*) ($n=6$) brain EPG and CPG compared with dolphin brain (*Tursiops truncatus* $n=2$) phosphoglycerides

	Zebra		Giraffe		Dolphin	
	CPG	EPG	CPG	EPG	CPG	EPG
18:2, $n-6$	1.22 (0.22)	0.14 (0.01)	1.18 (0.2)	1.07 (0.03)	1.8	0.2
20:2, $n-6$	0.11 (0.02)	0.10 (0.02)	0.25 (0.06)	0.23 (0.04)	0.1	0.1
20:3, $n-6$	1.15 (0.07)	0.89 (0.09)	0.55 (0.04)	0.40 (0.04)	0.1	0.1
20:4, $n-6$	5.33 (0.62)	10.6 (2.06)	6.01 (0.10)	13.2 (1.88)	4.5	8.6
22:4, $n-6$	1.15 (0.65)	4.28 (0.76)	1.43 (0.55)	5.12 (0.73)	0.8	2.7
22:5, $n-6$	0.84 (0.08)	2.11 (0.02)	0.52 (0.07)	2.09 (0.1)	0.4	1.3
Total $n-6$	9.8	19.1	8.9	22.1	7.7	13.0
18:3, $n-3$	1.14 (0.23)	1.55 (0.25)	0.80 (0.05)	0.41 (0.06)	0.4	0.3
20:5, $n-3$	0.24 (0.01)	0.26 (0.03)	0.14 (0.04)	0.13 (0.04)	0.2	0.8
22:5, $n-3$	1.94 (0.32)	0.95 (0.08)	1.82 (0.94)	0.61 (0.08)	0.9	1.5
22:6, $n-3$	3.84 (0.26)	19.4 (0.06)	4.59 (0.04)	22.4 (2.01)	4.3	29.0
Total $n-3$	7.16	22.2	7.35	23.5	5.8	31.6
Ratio $n-6:n-3$	1.4:1	1.1:2	1.3:1	1:1	1.3:1	1.2:4

setiferus). They also report that the arachidonic acid found would probably have been obtained via the diet. This data suggests a significant source in specialized aspects of the marine food chain, probably with coastal or shallow water origins. High levels of arachidonic acid (20:4, $n-6$) have also been reported in fish obtained from Australia (Sinclair *et al.*, 1983), suggesting a temperature effect. We have made similar observations on the liver oils of fish caught off the Tanzanian coast (Munhambo & Crawford, unpubl.). Most of the general data on fish lipids comes from cold water regions where the most highly unsaturated fatty acids (i.e. docosahexaenoic acid 22:6, $n-3$) become concentrated in the food chain. In warmer waters, this requirement for highly unsaturated $n-3$ fatty acids might be diminished.

The data on the zebra and dolphins illustrate the same principle for selection of $n-6$ fatty acids against an opposite concentration gradient. It is interesting that the balance of $n-6:n-3$ fatty acids in the adipose tissue of the zebra (0.17) was of the same order as that of the dolphin (0.22): the difference was in the chain length. The zebra $n-3$ fatty acid content was mainly alpha-linolenic acid, whereas in the case of the dolphin, the $n-3$ component consisted of 20 and 22 carbon chain-length fatty acids.

Certain seeds, such as those of balenites and the acacia, would provide larger quantities of oil and of linoleic acid than would be available from grass seeds. None the less, the giraffe

TABLE V

The ratio of n-6 to n-3 fatty acids determined in the stomach content, adipose fat, liver and brain phosphoglycerides of five land mammals and five species of dolphin. The data on koala and kangaroos were obtained from Naughton (1981), and that of the other species from our own study

Origin	Capuchin	Koala	Zebra	Giraffe	Grey kangaroo	Dolphin
Stomach	6:1	1:3	1:4	1:2	1:1	1:40
Fat	4:1	1:1.7	1:5.8	1.8:1	2:1	1:4.8
Liver						
CPG	5:1	13:1	8.9:1	5.7:1	2:1	1:1:1
EPG	2:1:1	9:1	7.2:1	2.1:1	3:1	1:2:1
Brain						
CPG	1.2:1	1.7:1	1.4:1	1.3:1	1.4:1	1:3:1
EPG	1:1	1:1	1:1.2	1:1	—	1:2.4

phosphoglycerides contained less linoleic and more arachidonic acid than those of the zebra. Despite the fact that the giraffe is a ruminant and eats green leaves, its tissue lipids were still dominated by the n-6 essential fatty acids. Naughton's (1981) information on leaf-eating marsupials (Table V) is of interest because it is the first data on marsupials and illustrates a similar selective phenomenon in favour of n-6 fatty acids, despite an n-3 rich food structure.

The evidence in the literature suggests that fish require n-3 fatty acids (Nicolaidis & Woodall, 1962; Cowey, 1976; Fujii & Yone, 1976; Yu & Sinnhuber, 1979) and that mammals require n-6 fatty acids. It is interesting that a concentrated source of linoleic acid was added to the land food chain following the evolution of flowering and seed-bearing plants toward the end of the Cretaceous period. Mammals evolved a requirement for linoleic acid and its derivatives and we found no evidence to suggest that dolphins need have lost that requirement. Evolution of the fishes would assumedly have taken place in the presence of a preponderance of the n-3 fatty acids: linoleic acid and its derivatives would have been relatively scarce during the earlier evolution of the fishes.

The zebra data offered no evidence that this species had adapted to an n-3 biology like the fish. Despite eating n-3 rich food, the n-6 fatty acids were found to dominate the tissue structural lipids. Naughton's (1981) data on the koala similarly suggests that dependence on n-6 fatty acids might have been established before the marsupials diverged from the eutherians.

Our data imply that dolphins are similar to land mammals in respect of their structural lipids. Hence, it is possible that dolphins may have a similar requirement for n-6 fatty acids and their eicosanoid derivatives, which are known to be associated with mammalian reproduction (Karim & Hillier, 1973) and regulation of several biological functions (Bunting, Moncada & Vane, 1983). It has been reported that alpha-linolenic acid (18:3, n-3) in high dietary amounts suppresses the metabolism of linoleic acid (18:2, n-6) (Holman, 1977), which makes it all the more surprising to find high concentrations of n-6 fatty acids in the dolphin structural lipids. We suggest that dolphins have adapted a specialized mechanism for concentrating the n-6 fatty acids; this could be through preferential selection or differences in rates of utilization. Similar mechanisms enable the rat to hold on tenaciously to small amounts of dietary n-3 fatty acids (Tinoco, Williams, Hincenbergs & Lyman, 1971) and differences in the efficiency of incorporation of individual

essential fatty acids have been reported (Sinclair & Crawford, 1972). There are also species differences in essential fatty acid metabolism (Rivers, Sinclair & Crawford, 1975; Cunnane, Keeling, Thompson & Crawford, 1984). These mechanisms, combined with behavioural selection of foods containing significant amounts of n-6 fatty acids, could explain the high proportions of arachidonic acid in dolphin tissue lipids.

The data suggests a consistent mammalian preference of n-6 essential fatty acids in the phosphoglycerides of structural tissue. The conclusion that there might be specific behavioural and biochemical selection for fatty acid types disposes of the conventional view that fats simply reflect the diet of an animal. This generalization may contain some truth for adipose tissue but not for cell membrane structural lipids. The contrasting food and tissue data in the giraffe, zebra and other species reported here suggest that the selection of n-6 fatty acids for structural purposes may be a general rule for mammalian species.

The fact that dolphins do not appear to have changed their allegiance to n-6 fatty acids on migration to the sea is of interest to evolutionary theory. We established that the lion, *Panthera leo* L. and the cat, *Felis catus* L. lacked significant, delta-6-desaturase (Rivers *et al.*, 1975; Rivers *et al.*, 1976; Frankel & Rivers, 1978; Frankel, 1980), which is the first step in the synthesis of arachidonic acid from linoleic acid. The animal focuses on preformed arachidonic acid from its diet rather than the parent n-6 fatty acid, linoleic acid and also requires preformed vitamin A as opposed to its vegetable precursor (Scott, 1968). This dependence on preformed derivatives could make it difficult for the cat to change evolutionary direction to a herbivorous diet. The data on dolphins offers similar evidence, suggesting that once locked in to a set of nutrient requirements, it is difficult to change.

The authors wish to express their appreciation to the United States Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Service, and to the Director, Dr I. Barrett, of the Southwest Fisheries Center, La Jolla, California for their invaluable help and advice. Thanks are also due to Mr L. J. Hansen and Mr J. R. Henderson who carried out the dissections of the dolphins. The organ samples were exported from the United States under USFWS permit number PRT 2-7202. We are also grateful to the Uganda Game Department and the Game Wardens in the District of Karamoja, including Mr S. Ruwheza and Mr S. Kabuye.

REFERENCES

- Ackman, R. G. (1969). Gas liquid chromatography of fatty acids and esters. In *Methods in enzymology* XIV: 329–381. New York & London: Academic Press.
- Ackman, R. G. (1982). Fatty acid composition of fish oils. In *Nutritional evaluation of long-chain fatty acids in fish oil*: 25–88. Barlow, S. M. & Stansby, M. E. (Eds). London: Academic Press.
- Ackman, R. G., Eaton, C. A. & Jangaard, P. M. (1965). Lipids of the fin whale (*Balaenoptera physalus*) from North Atlantic waters. I. Fatty acid composition of whole blubber and blubber sections. *Can. J. Biochem.* **43**: 1513–1520.
- Bowler, J. P. (1983). *The eclipse of Darwinism*. Baltimore, USA: Johns Hopkins University Press.
- Bunting, S., Moncada, S. & Vane, J. R. (1983). The prostacyclin-thromboxane A₂ balance: pathophysiological and therapeutic implications. *Br. Med. Bull.* **39**: 271–276.
- Burr, G. C. & Burr, M. M. (1930). On the nature and role of the fatty acids essential in nutrition. *J. Biol. Chem.* **86**: 587–621.
- Cowey, C. B. (1976). Use of synthetic diets and biochemical criteria in the assessment of nutrient requirements of fish. *J. Fish. Res. Canada* **33**: 1040–1045.
- Crawford, M. A. (1983). Background to essential fatty acids and their prostanoid derivatives. *Br. Med. Bull.* **39**: 210–213.
- Crawford, M. A., Casper, N. M. & Sinclair, A. J. (1976). The long chain metabolites of linoleic and linolenic acids in liver and brain of herbivores and carnivores. *Comp. Biochem. Physiol. (B)* **54**: 395–401.

- Crawford, M. A., Gale, M. M., Somers, K. & Hansen, I. L. (1970). Studies on plasma amino acids in East African adults in relation to endomyocardial fibrosis. *Br. J. Nutr.* **24**: 393–406.
- Crawford, M. A. & Sinclair, A. J. (1972). In *Lipids, malnutrition and the developing brain*: 267–275. Elliott, K. & Knight, J. (Eds). Amsterdam: Scientific Publs Assoc.
- Cunnane, S. C., Keeling, P. W. N., Thompson, R. P. H. & Crawford, M. A. (1984). Linoleic acid and arachidonic acid metabolism in human peripheral blood leucocytes: comparison with the rat. *Br. J. Nutr.* **51**: 209–217.
- Dougall, H. W., Drysdale, W. M. & Glover, P. E. (1964). The chemical composition of Kenya browse and pasture herbage. *E. Afr. Wildl. J.* **11**: 86–121.
- Fiennes, R. N. T-W., Hay, A. W. M., Watson, G., Crawford, M. A. & Hart, M. G. (1974). Linoleic acid deprivation in capuchin monkeys. *Proc. Nutr. Soc.* **33**: 49A.
- Fiennes, R. N. T-W., Sinclair, A. J. & Crawford, M. A. (1973). Essential fatty acid studies in primates. Linolenic acid requirements of capuchins. *J. Med. Prim.* **2**: 155–169.
- Fitch, J. E. & Brownell, R. L., Jr (1968). Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. *J. Fish. Res. Bd Canada* **25**: 2561–2574.
- Flanigan, N. J. (1972). The central nervous system. In *Mammals of the sea. Biology and medicine*: 215–246. Ridgeway, S. H. (Ed.). Illinois, USA: C. C. Thomas.
- Folch, J., Lees, M. & Stanley, G. H. S. (1957). A simple method for the isolation and purification of total lipids from animal tissue. *J. Biol. Chem.* **226**: 497–509.
- Frankel, T. L. (1980). *Essential fatty acid deficiency in the cat (Felis catus L.)*. PhD Thesis, The University of Cambridge.
- Frankel, T. L. & Rivers, J. P. W. (1978). The nutritional and metabolic impact of gamma-linolenic acid (18:3, n-6) on cats deprived of animal lipid. *Br. J. Nutr.* **39**: 227–231.
- Fujii, M. & Yone, Y. (1976). Studies on nutrition of red sea bream. XIII. Effect of dietary linolenic acid and w3 polyunsaturated fatty acids on growth and feed efficiency. *Bull. Jap. Soc. scient. Fish.* **42**: 583–588.
- Gingerich, P. D., Wells, N. A., Russell, D. E. & Ibrahim Shah, S. M. (1983). Origin of whales in epicontinental remnant seas. *Science, Wash.* **220**: 403–406.
- Glaessner, M. F. (1984). *The dawn of animal life*. London: Cambridge University Press.
- Hitchcock, C. & Nichols, B. W. (1971). *Plant lipid biochemistry*: 81–93. New York: Academic Press.
- Holman, R. T. (1977). *Polyunsaturated fatty acids*: 163–182. Kunau, W. H. & Holman, R. T. (Eds). Champaign, Illinois: Am. Oil Chem. Soc.
- Karim, S. M. M. & Hillier, K. (1973). *The prostaglandins*: 167–200. Cuthbert, M. F. (Ed.). London: William Heinemann.
- Kulu, D. D. (1972). Evolution and cytogenetics. In *Mammals of the sea. Biology and medicine*: 503–527. Ridgeway, S. H. (Ed.). Illinois, USA: C. C. Thomas.
- Lilly, M. L. & Bottino, N. R. (1981). Identification of arachidonic acid in Gulf of Mexico shrimp and degree of biosynthesis in *Penaeus setiferus*. *Lipids* **16**: 871–875.
- McColl, J. D. & Rossiter, R. J. (1951). Lipids of the nervous system of the squid *Loligo pealii*. *J. exp. Biol.* **28**: 116–124.
- Naughton, J. (1981). *The polyunsaturated lipids of brain and other tissues of Victorian marsupial and monotreme species*. Thesis for Master of Applied Science, Footscray Institute of Technology, Melbourne, Australia.
- Nicolaides, N. & Woodall, A. N. (1962). Impaired pigmentation in chinook salmon fed diets deficient of EFA. *J. Nutr.* **78**: 431–437.
- Nolan, C. & Margolaish, E. (1968). Comparative aspects of primary structures of proteins. *A. Rev. Biochem.* **37**: 727–790.
- Ridgeway, S. H. (1972). Homeostasis in the aquatic environment. In *Mammals of the sea. Biology and medicine*: 590–745. Ridgeway, S. H. (Ed.). Illinois, USA: C. C. Thomas.
- Rivers, J. P. W., Hassam, A. G., Crawford, M. A. & Brambell, M. R. (1976). The inability of the lion, *Panthera leo* L. to desaturate linoleic acid. *FEBS Lett.* **67**: 269–270.
- Rivers, J. P. W., Sinclair, A. J. & Crawford, M. A. (1975). Inability of the cat to desaturate essential fatty acids. *Nature, Lond.* **258**: 171–173.
- Romer, A. S. (1967). *Vertebrate paleontology*. Chicago: The University of Chicago Press.
- Sargent, J. R. (1976). *Biochemical and biophysical perspectives in marine biology* **13**. Malins, D. C. & Sargent, J. R. (Eds). New York: Academic Press.
- Scott, P. P. (1968). The special features of nutrition of cats, with observations on wild Felidae nutrition in the London Zoo. *Symp. zool. Soc. Lond.* No. 21: 21–36.
- Sinclair, A. J. (1975). The incorporation of radioactive polyunsaturated fatty acids into the liver and brain of the developing rat. *Lipids* **10**: 175–184.
- Sinclair, A. J., O'Dea, K. & Naughton, J. M. (1983). Elevated levels of arachidonic acid in fish from northern Australian coastal waters. *Lipids* **18** (12): 877–881.

- Sinclair, A. J. (1975). The incorporation of radioactive polyunsaturated fatty acids into the liver and brain of the developing rat. *Lipids* **10**: 175-184.
- Stirton, R. A. (1959). *Time life and man*. New York: John Wiley & Sons
- Tinoco, J., Williams, M. A., Hincenbergs, I. & Lyman, R. L. (1971). Evidence for non-essentiality of linolenic acid in the diet of the rat. *J. Nutr.* **101**: 937.
- Williams, G. (1981). Dietary deficiencies of captive dolphins. *Progr. Lipid Res.* **20**: 259-260.
- Williams, G., Davidson, D. C., Stevens, P. A. & Crawford, M. A. (1977). Comparative fatty acids of the dolphin and the herring. *J. Am. Oil Chem. Soc.* **54**: 328-330.
- Yu, T. C. & Sinnhuber, R. O. (1979). Effect of dietary w3 and w6 fatty acids on growth and feed conversion efficiency of Coho salmon (*Oncorhynchus kisutch*). *Aquaculture* **16**: 31-38.

THE RELATIVE MAGNITUDE OF THE 1986 PACIFIC SARDINE SPAWNING BIOMASS OFF CALIFORNIA

PATRICIA WOLF

California Department of Fish and Game
245 West Broadway
Long Beach, California 90802

PAUL E. SMITH

National Marine Fisheries Service
Southwest Fisheries Center
P.O. Box 271
La Jolla, California 92038

CHERYL L. SCANNELL

California Department of Fish and Game
245 West Broadway
Long Beach, California 90802

ABSTRACT

The spawning biomass of the Pacific sardine off southern California during 1986 remains at or above 20,000 short tons¹. This determination was made using an egg production area method, which estimates the area over which eggs of a specified spawning biomass (20,000 short tons) would be expected to occur. The area method was developed from the egg production method, which estimates adult biomass from measurements of egg production in the spawning area and from the egg production rate of the adult population. From estimates of components of egg production rate and specific fecundity for sardines, we expected that 20,000 tons of spawning biomass would cover a spawning area of about 500 n.mi².

The August 1986 survey extended from Point Conception to San Diego and ranged from the 10-fathom isobath to offshore approximately 25 miles. A total of 266 sardine eggs was collected at 59 of 330 stations. Spawning extended from Santa Barbara to Dana Point and out to the Santa Barbara Channel Islands and Santa Catalina Island, and covered an estimated 955 n.mi². This spawning area is 43% larger than the spawning area observed in 1985.

RESUMEN

En 1986, la biomasa de desove de la sardina del Pacífico frente a California del Sur se mantuvo en o por encima de las 20,000 toneladas cortas¹. Esta determinación fue hecha mediante el método del área de producción de huevos, el cual estima el área en la cual se espera encontrar los huevos correspondientes a una determinada biomasa de desove (20,000 toneladas cortas). El método del área se basó en la método de producción de huevos el cual estima la biomasa de los adultos a partir de las mediciones de producción de huevos en el área de desove y de la tasa de producción de huevos de la población adulta. Dadas las estimaciones de com-

ponentes de la tasa de producción de huevos y la fecundidad específica de las sardinas, esperábamos que 20,000 toneladas de biomasa de desove cubrieran un área de desove de aproximadamente 500 millas náuticas².

El muestreo realizado en agosto de 1986 se extendió desde Point Conception hasta San Diego y cubrió desde la isóbata de 10 brazas hasta 25 millas mar adentro. Un total de 226 huevos de sardina fue colectado en 59 de las 330 estaciones. El desove abarcó desde Santa Barbara hasta Dana Point y, mar adentro, hasta las islas del canal de Santa Barbara y la isla Santa Catalina y, se estimó que cubrió 955 m.n². Este área de desove es un 43% más extensa que la observada en 1985.

INTRODUCTION

In this report we evaluate the magnitude of the 1986 spawning biomass of the Pacific sardine relative to 20,000 tons. The California Department of Fish and Game (CDFG) is required to determine annually whether the spawning biomass is above or below this level. Earlier assessments of the spawning biomass were based on ichthyoplankton surveys, incidental landings in mackerel and live bait fisheries, trawl surveys, and aerial observations. From 1974 through 1985, a moratorium on the fishing of sardines was in effect because the biomass remained below 20,000 tons.

The egg production area technique was developed (Wolf and Smith 1985) and applied to sardines in 1985 (Wolf and Smith 1986). This technique allows an objective determination of whether the spawning biomass has exceeded 20,000 tons. The Pacific sardine fishery was reopened in 1986 with a 1,000-ton quota, since regulations permit a low rate of mortality due to fishing (.05) when the spawning stock recovers to 20,000 tons.

We used the egg production area technique to assess the relative magnitude of the sardine spawning biomass during 1986. Details of the method, including procedures for estimating egg production parameters, are described in Wolf and Smith (1986). An adult survey was conducted simultane-

¹Commercial landings, tonnages specified in legislation, and tonnages in this paper are reported in short tons.

[Manuscript received February 5, 1987.]

ously with the egg area survey, in order to develop current estimates of adult parameters for Pacific sardines. Results from this survey, however, are not yet available. Design and results of the 1986 egg survey are presented in the following sections.

EGG PRODUCTION METHOD

The egg production method (Lasker 1985) was developed by Parker (1980) and applied by Picquelle and Hewitt (1983, 1984) and Hewitt (1984) to estimate northern anchovy biomass. This method estimates spawning biomass as

$$B = P_o A \frac{kW}{RFS}$$

where B = spawning biomass (MT),
 P_o = daily egg production, number of eggs produced per 0.05 m² of sea-surface area,
 W = average weight of mature females (g),
 R = sex ratio, fraction of population that is female, by weight (g),
 F = batch fecundity, number of eggs spawned per mature female per batch,
 S = fraction of mature females spawning per day,
 A = total area of survey (0.05 m²), and
 k = conversion factor from grams to metric tons.

EGG PRODUCTION AREA METHOD

In the egg production area method, the spawning biomass is specified and the equation solved for A_1 :

$$A_1 = \frac{B_1 R F S m}{P_o k_1 W}$$

where A_1 = spawning area of biomass B_1 in nautical miles²,
 B_1 = spawning biomass, in short tons,
 k_1 = conversion factor from grams to tons,
 m = conversion factor from 0.05 m² to nautical miles².

In the egg production method, daily egg production and population fecundity parameters are measured during the survey. Daily production of eggs, P_o , is estimated from the density and embryonic developmental stages of eggs collected in an ichthyoplankton survey. Daily specific fecundity parameters W , F , S , and R are estimated from samples of adult fish collected during the survey.

In the egg production area method, we adapted existing information from previous studies (Table 1) concerning sardines and related species to estimate parameters P_o , W , F , S , and R for sardines. This range of parameter estimates—presented and described in Wolf and Smith (1986)—was used in the egg production area equation to produce a range of estimates of A_1 . We selected 500 n.mi² from the range of values as a useful estimate of spawning area.

SURVEY DESIGN

The 1986 survey was conducted in August, rather than in May, as in 1985. Several sources of information, including nearshore egg and larval surveys in the Southern California Bight (R.J. Lavenberg, Los Angeles County Museum of Natural History, pers. comm.) indicated that sardine spawning in recent years has occurred in late summer and fall rather than in spring. CDFG surveys of young fish did not detect evidence of sardine recruitment until September 1985. Adult sardines captured in these sea surveys and incidentally in

TABLE 1
Values of Parameters Used to Estimate Spawning Area, and Resulting Estimates

B_1	W	R	F	P_o	S	A_1
Spawning biomass (short tons)	Average female weight (g)	Sex ratio (females/total)	Batch fecundity (eggs/batch/ female)	Egg production (eggs/.05m ² -day)	Spawning fraction (spawning females/ total females)	Spawning area (nautical miles ²)
20,000	120	0.5	32,000	5.0	0.02	141
					0.05	353
					0.10	706
					0.15	1,058
				1.5	0.02	470
					0.05	1,176
					0.10	2,352
					0.15	3,528

the mackerel fishery were in progressively more advanced prespawning states in summer and fall during 1985.

The location of the survey area was based on results of the 1985 survey, which indicated that sardine spawning took place relatively close to shore and was prevalent in the eastern portion of the Santa Barbara Channel. Stations were more concentrated in 1986, and were spaced 4 n.mi. apart offshore and 4 n.mi. alongshore, in an attempt to obtain a greater number of positive stations to improve information on the sampling distribution of eggs. The survey covered approximately 5,000 n.mi². As in 1985, the critical spawning area, A_1 , was estimated to be 500 n.mi², or approximately 10% of the 1986 survey area. Because each station represented 16 n.mi², the calculated spawning area that 20,000 tons of sardines would cover was expected to produce at least 31 stations with eggs present.

SURVEY DESCRIPTION

The survey was conducted aboard the Occidental College research vessel *Vantuna*, from August 4 through August 12, 1986. Stations were occupied north to south from Point Conception to the Mexican border, from the 10-fathom isobath to approximately 25 n.mi. offshore (Figure 1). Samples were

collected at all hours, and, in contrast to the 1985 survey, stations occurring within shipping lanes were occupied. Plankton samples were collected at 330 stations using a 25-cm-diameter CalVET net (vertical egg tow) of 150-micron mesh. The net was retrieved vertically from 70 meters where depth allowed. Plankton samples were preserved in 5% buffered Formalin solution at sea. In the laboratory, sardine and anchovy eggs and larvae were identified, sorted, and counted.

The 1986 survey collected a total of 266 sardine eggs from 59 stations, with the number of eggs per station ranging from 1 to 18 (Figure 2). The mean number of eggs per station was 4.51 (standard error = 0.548) (Table 2). Positive stations occurred along the coast between Santa Barbara and Ventura; in the eastern portion of the Santa Barbara Channel out to and around Santa Cruz Island; in Santa Monica Bay and offshore in the Santa Monica Basin to approximately 30 miles; and between Sea! Beach and Dana Point, along the coast and out to Santa Catalina Island in the San Pedro Channel. A total of 413 sardine larvae was collected at 113 stations, from approximately the same areas as sardine eggs (Figure 3). The number of sardine larvae per positive tow ranged from 1 to 22.

Evidence of anchovy spawning was much less

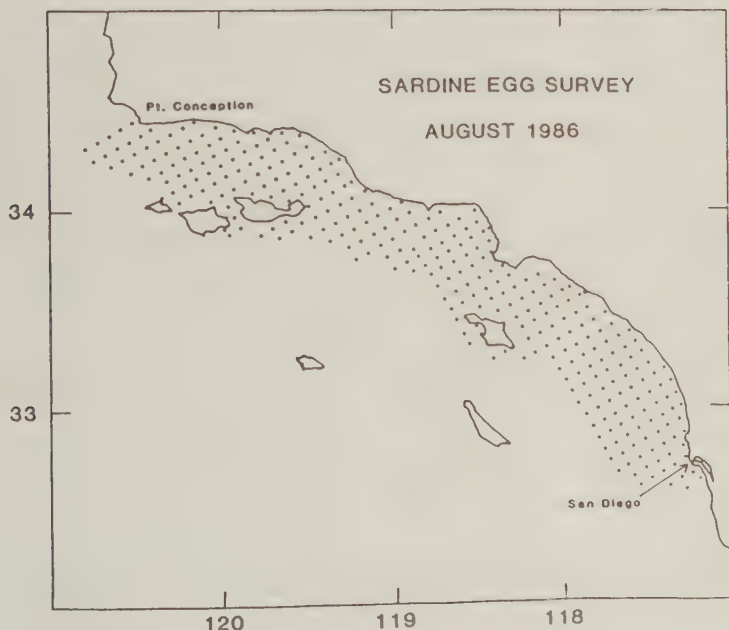


Figure 1. Stations occupied during sardine survey, August 1986

TABLE 2
 Pacific Sardine Egg Sample Frequency Distributions at Different Levels of Estimated Spawning Biomass*

		Net types and years						
x	$\ln(x)$	CalVET 1986	CalVET 1985	CDFG 2-m 1931-32	1-m 1941	0.5-m 1941	Hi-speed 1950	1-m 1959
.125	-2.08	— ^b	—	2	—	—	—	—
.5	-0.69	—	—	4	—	—	—	—
2	0.69	—	—	6	21	—	—	28
8	2.08	—	—	7	22	8	—	28
32	3.47	—	—	14	16	15	—	30
128	4.85	19	4	12	31	29	77	23
512	6.24	22	4	13	27	14	20	12
2,048	7.62	18	2	5	17	10	7	5
8,192	9.01	0	1	2	3	2	1	4
Estimated mean (Biomass (10 ⁶ MT) ^c)		902	1,564	544	569	619	406	410
		0.02	0.02	3.9	2.7	2.7	1.0	0.2

* (Smith and Richardson 1977)

^b Value below sampler threshold

^c (Murphy 1966)

common, probably because most anchovy spawning occurs in February and March. Only 39 eggs and 240 larvae were collected, from 27 and 106 stations, respectively. Furthermore, anchovy eggs and larvae were more concentrated in the southern portion of the survey area, between Point Fermin and San Diego.

SPAWNING AREA

The spawning area was determined by multiplying the number of positive egg stations by the area represented by each station (16 n.mi²). Slight adjustments were made by including half of the unsampled areas that were adjacent to positive stations, averaged along lines by order of occupation.

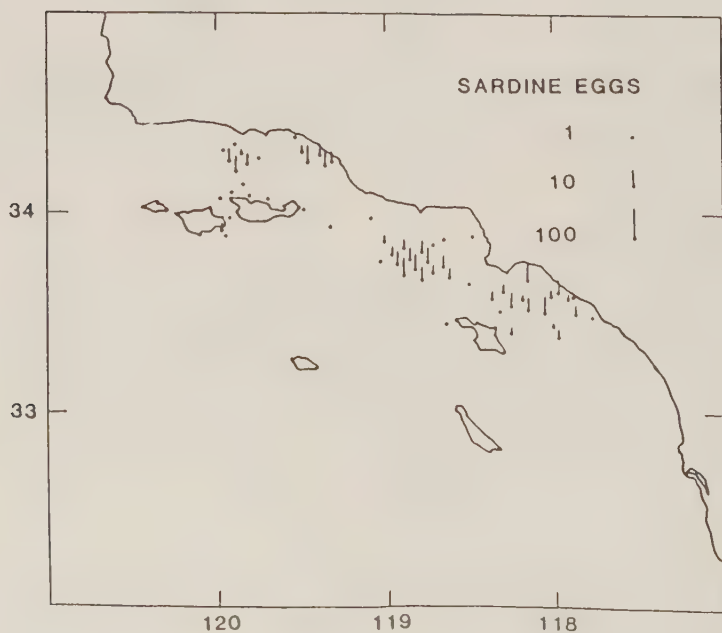


Figure 2. Stations with sardine eggs

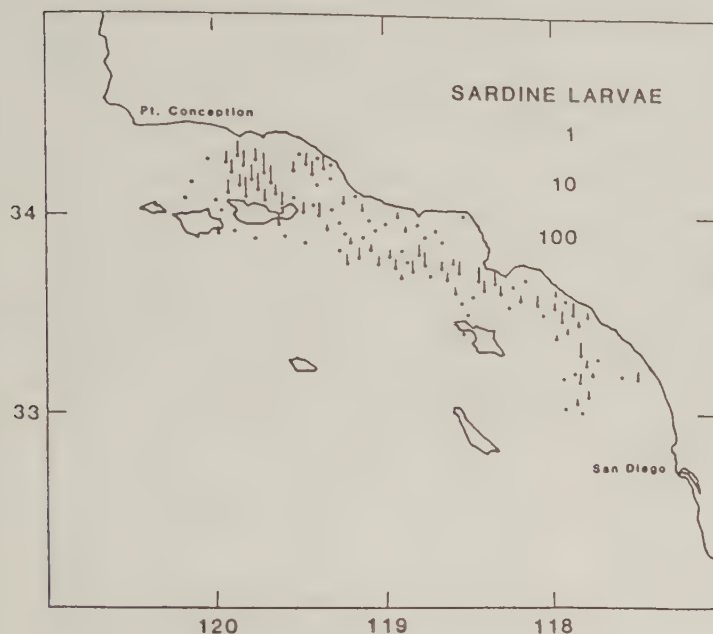


Figure 3. Stations with sardine larvae.

The area of positive stations too near to shore to include an entire 16 n.mi². was also adjusted to include only the portion actually sampled (Figure 4). The adjusted estimate of the 1986 spawning area is 955 n.mi²., which is within the range of spawning area calculated for 20,000 tons of spawning biomass, and greater than the selected estimate of 500 n.mi². for A_1 . This year's spawning area is 43% larger than the spawning area determined in May 1985.

DISCUSSION

Because the spawning area detected during the survey exceeds that predicted for 20,000 tons of adult sardines, the spawning biomass of sardines off California is considered to be at least 20,000 tons. As a result, the 1,000-ton fishery for sardines was reopened on January 1, 1987. This is the second year of a limited fishery for sardines, and is a continuation of the first directed harvest of sardines allowed in California since the moratorium was enacted 12 years ago.

Although a substantial (43%) increase in spawning area was observed in 1986 compared to the spawning area detected in 1985, the estimate of spawning area for 1986 is probably conservative. Our observations were limited to the survey area, and additional spawning probably occurred else-

where. We observed evidence of spawning at the offshore edge of the survey, and spawning could have extended beyond those bounds. Fishermen reported large schools of sardines near Santa Barbara Island at the time of the survey. The offshore banks (Tanner and Cortez) were historical spawning grounds for sardines and, although we saw no evidence of spawning there in 1985, it is not known whether spawning occurred in those areas during the 1986 survey. CDFG young-fish surveys in October 1986 detected juvenile sardines near Tanner Bank. Young-of-the-year sardines were observed in Monterey Bay in 1985, and in San Francisco Bay in 1986, indicating that some spawning occurred north of Point Conception in both years.

Our estimate of spawning area for 20,000 tons of adults (500 n.mi².) is based on estimates of the adult reproductive parameters. Daily egg production and spawning fraction are not yet known for Pacific sardines. Two other parameters—average female weight and batch fecundity—were estimated from the historical population. An adult survey, in which sardines were collected by purse seine, was conducted simultaneously with the egg survey during 1986 in order to improve our estimates of these parameters. Results from this survey, however, are not yet available. At low biomass levels, existing techniques for biomass

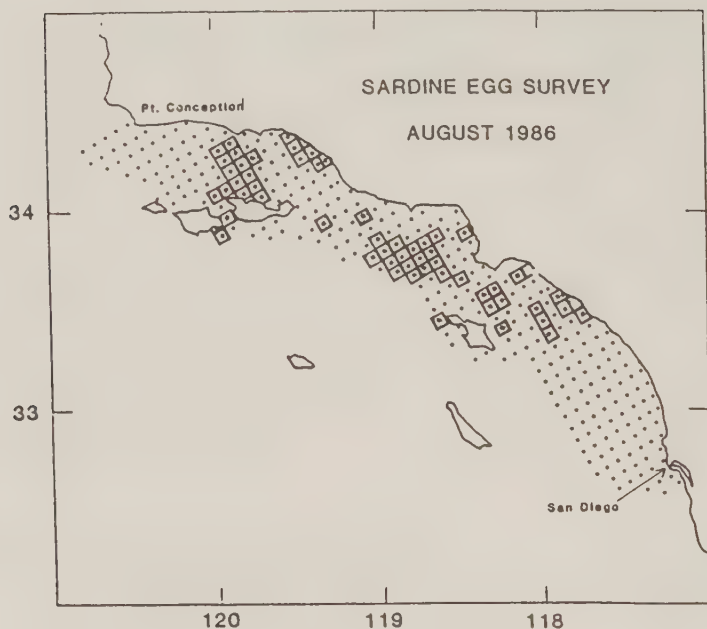


Figure 4. Squares outline the 4-by-4-n.mi. areas represented by each positive station in order to illustrate the spawning area adjustment. Shaded area is the adjusted sardine spawning area.

estimation cannot provide adequate precision. Evaluation of spawning area for biomass assessment is the best available tool where there are low levels of a recovering stock. For sardines, however, the actual relationship between spawning biomass and spawning area is not yet known.

Although the estimated mean of positive samples in the CalVET surveys is high relative to samples taken in the 1930s and 1950s, the 1986 estimated mean appears to be more realistic. This reflects the increased number of positive samples, but still points to technical problems (sampling threshold and scale of integration of the CalVET net relative to other samplers) that cannot be resolved with small numbers of samples.

ACKNOWLEDGMENTS

We thank the crew of the Occidental College RV *Vantuna* and the captain, M. Kibby. B. Flerx and D. Abramenkoff of the National Marine Fisheries Service (NMFS) provided assistance with cruise logistics and equipment. The scientific crew participating in the cruise included A. Enami, G. Lang, J. Patman, and P. Simon of Occidental College, L. Dunn, M.A. Lumpkin, M.E. Farrell, F.R. Pocinich, and M.J. Haddox of Scripps Institution

of Oceanography sorted the CalVET plankton samples, and B. Sumida MacCall, E.M. Acuna, E.G. Stevens, and D.A. Ambrose of NMFS staged the sardine eggs under the supervision of Dr. H.G. Moser. C.S. Methot and C. Meyer of NMFS entered and edited the data.

LITERATURE CITED

- Hewitt, R.P. 1984. The 1984 spawning biomass of the northern anchovy. SWFC Admin. Rep. LJ-84-18, 17 p.
- Lasker, R., ed. 1985. An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy (*Engraulis mordax*). U.S. Dep. Commer. NOAA Tech. Rep. NMFS 36, 99 p.
- Murphy, G.I. 1966. Population biology of the Pacific sardine (*Sardinops caerulea*). Proc. Calif. Acad. Sci. 34:1-84.
- Parker, K. 1980. A direct method for estimating northern anchovy, *Engraulis mordax*, spawning biomass. Fish. Bull., U.S. 78:541-544.
- Picquelle, S.J., and R.P. Hewitt. 1983. The northern anchovy spawning biomass for the 1982-83 California fishing season. Calif. Coop. Oceanic Fish. Invest. Rep. 24:16-28.
- . 1984. The 1983 spawning biomass of the northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 25:16-27.
- Smith, P.E., and S.L. Richardson. 1977. Standard techniques for pelagic fish egg and larva surveys. FAO Tech. Paper No. 175, 100 p.
- Wolf, P., and P.E. Smith. 1985. An inverse egg production method for determining the relative magnitude of Pacific sardine spawning biomass off California. Calif. Coop. Oceanic Fish. Invest. Rep. 26:130-138.
- . 1986. The relative magnitude of the 1985 Pacific sardine spawning biomass off southern California. Calif. Coop. Oceanic Fish. Invest. Rep. 27:25-31.

RELATIONSHIP OF OTOLITH LENGTH TO TOTAL LENGTH IN ROCKFISHES FROM NORTHERN AND CENTRAL CALIFORNIA

Knowing the relationship between otolith length and total length of a fish is useful for two reasons: 1) Fish size can be estimated from otolith lengths measured from otoliths encountered in predator stomachs, in core samples, archaeological sites, etc., and 2) the length of a fish can be verified when the age determined from the otolith lies outside expected values.

The otolith/total length relationship is useful in predator-prey and archeological studies if fish size can be extrapolated from otolith length. Otoliths are often the only part of a prey fish remaining in a predator's gut (Ainley et al. 1981; Treacy and Crawford 1981) or at cooking sites of archeological middens (Fitch 1972). Fish lengths could be estimated from otoliths found as remains of prey or in coastal archaeological excavations (Fitch and Brownell 1968). Existing keys (e.g., Morrow 1979) allow identification of fish species from otoliths. With these keys, personal reference collections, and the length relationships described in this paper, investigators will be able to verify species and size data collected in field sampling, and obtain more complete knowledge of prey species of marine mammals, birds, and fishes.

Large-scale surveys, such as the California cooperative survey (Sen 1984) that samples commercial rockfish landings in northern California, are prone to errors at several levels. Problems that may be encountered in collecting otoliths and measuring fish lengths include errors in recording lengths and the mixing up of otoliths. Some errors can be corrected by measuring the otolith and estimating the size of the fish it came from. Every effort should be made to eliminate erroneous data from the database before curves are constructed or cohort analysis is performed.

In this paper, I report the results of my investigation of the relationship between otolith length and total length for 30 rockfish species of the genus *Sebastes*. Linear regression statistics are presented for all fish of the species encountered.

Methods

Specimens were collected during a life history study on the rockfishes of northern and central California conducted at the Southwest Fisheries Center Tiburon Laboratory. Fish were sampled from the commercial trawl fishery, the commercial sport fishery, skiffs, and research cruises from 1977 to 1980. Specimens were identified to species, and then total lengths of frozen—then thawed—carcasses were measured on a meter board in millimeters (mm). Otoliths were measured to the nearest 0.1 mm with an ocular micrometer. The greatest length of the otolith was measured from the anterior tip to the most posterior projection (Kimura et al. 1979) (Fig. 1) as if the otolith were flat, without compensating for the curvature. Linear regressions were run on total length (y) versus otolith length (x) for 30 rockfish species. Outliers (± 3.0 standard deviations) from the line were assumed to result from measurement or recording errors and were discarded (2% of the observations).



FIGURE 1.—The length of an otolith is measured from the anterior tip to the posterior projection.

Table 1 gives the sample size (N) and the minimum and maximum total lengths used in the analysis for each species and each sex. Table 2 shows estimates of y -intercept (a), slope (b), standard error of estimate ($S_{y.x}$), correlation coefficient (r), and F for each species and sex. Analysis of covariance was used to determine if separate lines for males and females significantly reduced the variance from a common line (Kleinbaum and Kupper 1978). Analysis of covariance was also used to test for significant differences in the relationship of otolith length to total length between the sexes at the $P = 0.05$ level and the $P = 0.01$ level (Table 2). The highest values of r and examination of scattergrams (Fig. 2) indicate that the length relationships are linear over the observed range of values. Limiting the application of these regressions to the ranges of observed values is advised.

Results and Discussion

Linear regressions were run on each sex in order to investigate possible sexual differences. In 17 of the 30 species investigated, the relationship between otolith length and fish length is significantly different between males and females (Table 2). Sexual size dimorphism has been observed in 11 of the 17 species in Table 2. These species (plus *S. alutus*) include most commercially and sport-caught rockfishes in the northeastern Pacific Ocean. The six species for which growth curves have yet to be con-

TABLE 1.—Sample sizes and size ranges used in the linear regressions of total length versus otolith length for *Sebastes*. Measurements are in millimeters.

Species of <i>Sebastes</i>	N	Males		N	Females	
		Total length			Total length	
		Mini- mum	Maxi- mum		Mini- mum	Maxi- mum
<i>auriculatus</i>	34	257	477	44	179	523
<i>aurora</i>	27	203	378	44	230	398
<i>carnatus</i>	100	112	289	103	109	279
<i>caurinus</i>	67	281	507	65	135	542
<i>chlorostictus</i>	73	155	450	101	162	458
<i>chrysomelas</i>	72	162	256	94	141	268
<i>constellatus</i>	54	186	422	45	177	430
<i>crameri</i>	42	206	445	47	134	505
<i>diploproa</i>	34	125	343	44	131	381
<i>elongatus</i>	25	188	326	73	135	378
<i>entomelas</i>	38	245	464	68	284	524
<i>flavidus</i>	163	254	504	221	232	539
<i>goodei</i>	26	227	385	52	227	556
<i>hopkinsi</i>	13	119	195	46	134	294
<i>jordanii</i>	118	147	281	65	160	321
<i>levis</i>	14	267	773	15	237	900
<i>maliger</i>	13	317	481	21	226	478
<i>melanops</i>	120	334	534	89	197	607
<i>melanostomus</i>	34	250	442	46	297	538
<i>miniatus</i>	64	328	644	35	360	691
<i>mystinus</i>	141	248	480	63	213	375
<i>nebulosus</i>	25	270	391	23	257	500
<i>ovalis</i>	18	228	355	66	241	456
<i>paucispinis</i>	46	287	733	40	296	786
<i>pinniger</i>	92	249	585	81	251	622
<i>rosaceus</i>	72	212	426	75	203	310
<i>ruberrimus</i>	52	257	695	50	245	678
<i>saxicola</i>	29	141	240	73	159	358
<i>semicinctus</i>	15	125	150	16	128	182
<i>serranoides</i>	60	235	469	70	229	528

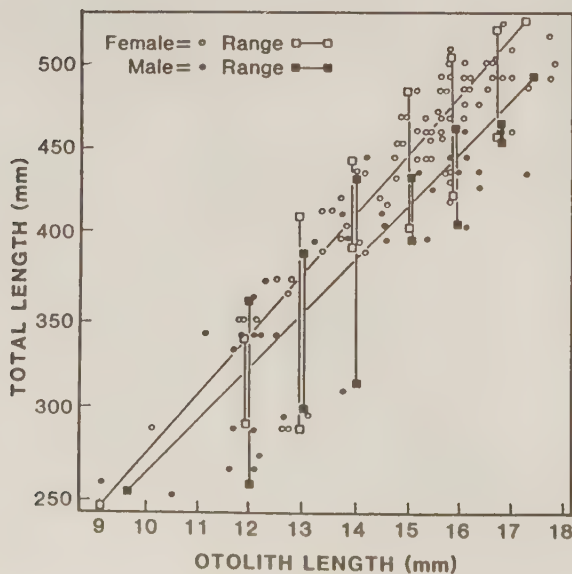


FIGURE 2.—Linear regression of total length on otolith length of widow rockfish, *Sebastes entomelas*. The range of values for males (•-•) and females (o-o) at each whole millimeter of otolith length.

TABLE 2.—Results of linear regressions of total length (y) versus otolith length (x) for *Sebastes*. Measurements are in millimeters. The F -test was run using the sums squared from the analysis of covariance comparing males and females; * - $P = 0.05$, ** - $P = 0.01$.

Species of <i>Sebastes</i>	Males				Females				
	r	a	b	$S_{y,x}$	r	a	b	$S_{y,x}$	F
<i>crameri</i> ^{1,2}	0.926	19.270	24.629	22.054	0.988	-43.418	29.440	16.067	4.676*
<i>diploproa</i> ^{3,2}	0.980	1.282	21.090	12.686	0.985	-22.120	23.717	13.390	6.601**
<i>entomelas</i> ^{1,2,4}	0.871	-23.039	28.853	33.896	0.880	-51.835	32.452	28.968	6.243**
<i>flavidus</i> ^{1,2,5,6}	0.923	30.400	23.546	14.771	0.947	-12.604	26.901	18.389	25.637**
<i>goodei</i> ⁷	0.975	1.696	23.866	12.741	0.987	-56.831	29.347	16.321	14.842**
<i>hopkinsi</i>	0.868	20.734	20.172	9.567	0.951	-10.895	26.890	10.999	9.172**
<i>maliger</i>	0.840	79.427	21.359	25.533	0.965	-105.649	33.479	19.259	4.221*
<i>melanops</i> ^{5,6}	0.912	5.472	27.070	18.456	0.949	-124.076	35.784	19.480	25.338**
<i>melanostomus</i>	0.907	-21.094	25.187	21.777	0.918	-21.713	26.211	23.405	8.441**
<i>miniatus</i>	0.961	-42.615	28.385	23.399	0.971	-72.278	30.607	24.103	4.638*
<i>mystinus</i> ^{6,7}	0.910	-2.255	28.987	23.112	0.881	60.010	22.054	14.965	3.643**
<i>ovalis</i>	0.903	26.185	24.964	13.268	0.963	-27.207	31.859	14.144	21.995**
<i>paucispinis</i> ^{1,8}	0.893	-51.911	38.441	55.433	0.931	-102.932	43.993	56.501	5.965**
<i>pinniger</i> ^{1,2,5}	0.950	-61.508	27.663	25.655	0.967	-95.891	30.455	29.004	8.200**
<i>saxicola</i> ¹	0.928	-0.111	19.074	7.544	0.974	-19.565	22.495	12.797	11.412**
<i>semicinctus</i>	0.880	34.331	16.015	4.061	0.938	12.022	21.372	4.981	20.081**
<i>serranoides</i> ^{6,9}	0.967	-5.307	25.898	13.462	0.969	-63.475	30.445	20.668	10.318**

¹Westrheim and Harling 1975.

²Shaw and Archibald 1981.

³Boehlert and Kappenman 1980.

⁴Lenarz 1987.

⁵Six and Horton 1977.

⁶Wyllie Echeverria 1986.

⁷Miller and Geibel 1973.

⁸Wilkins 1980.

⁹Love and Westphal 1981.

structed may also show sexually size-dimorphic growth.

The 13 species with no difference noted between males and females consist primarily of two closely related taxonomic groups (Barsukov 1981). Few growth studies exist for these species. The first group of shallow, nearshore species is represented in this study by *S. auriculatus*, *S. carnatus*, *S. caurinus*, *S. chrysomelas*, and *S. nebulosus*. The growth curve for *S. chrysomelas* is the same for males and females (Zaitlan 1986). The second group is the subgenus *Sebastomus* (Chen 1971), represented in this study by *S. chlorostictus*, *S. constellatus*, and *S. rosaceus*. Growth curves exist for two members: *S. helvomaculatus* (Westrheim and Harling 1975) and *S. umbrosus* (Chen 1971), which do not show sexual size dimorphism. The indications are relationships of otolith length to total length reflect the age-at-length relationship between the sexes.

In food-habit studies, otoliths are often found but the sex and length of the fish are not known. Table 3 shows regressions for the combined sexes for those occasions when the sex is unknown or when the regressions were not significantly different between the sexes.

Data analysis for *S. entomelas* shows a potential to derive estimates of age from otolith lengths (Fig. 3). The calculated total lengths for males and females for each 1 mm increment in otolith length are overlaid on the age-length curve (from Lenarz 1987). These relationships are species-specific and

TABLE 3.—Results of linear regressions of total length (y) versus otolith length (x) for *Sebastes* for sexes combined. Measurements are in millimeters.

Species of <i>Sebastes</i>	r	a	b	$S_{y,x}$
<i>auriculatus</i>	0.968	-53.032	33.159	17.729
<i>aurora</i>	0.782	15.124	19.910	24.818
<i>carnatus</i>	0.945	-39.365	30.573	10.258
<i>caurinus</i>	0.906	5.099	30.234	26.291
<i>chlorostictus</i>	0.974	-18.537	24.113	14.898
<i>chrysomelas</i>	0.919	-21.780	28.609	9.020
<i>constellatus</i>	0.978	-37.484	25.266	13.123
<i>crameri</i>	0.971	-27.098	28.104	19.912
<i>diploproa</i>	0.980	-12.854	22.635	14.020
<i>elongatus</i>	0.974	-13.564	24.020	12.284
<i>entomelas</i>	0.898	-6.890	33.113	32.247
<i>flavidus</i>	0.938	-10.946	26.506	18.158
<i>goodei</i>	0.983	-57.996	29.129	17.819
<i>hopkinsi</i>	0.957	-30.546	28.868	12.168
<i>jordani</i>	0.985	-2.313	22.096	7.353
<i>levis</i>	0.973	-170.108	47.458	46.975
<i>maliger</i>	0.928	-53.107	29.967	23.862
<i>melanops</i>	0.930	-48.222	30.557	21.002
<i>melanostomus</i>	0.928	-47.070	27.362	23.590
<i>miniatus</i>	0.962	-56.738	29.365	24.516
<i>mystinus</i>	0.912	-18.175	29.765	23.204
<i>nebulosus</i>	0.891	32.970	25.181	16.131
<i>ovalis</i>	0.952	-53.472	33.562	17.179
<i>paucispinis</i>	0.903	-77.089	41.089	59.143
<i>pinniger</i>	0.957	-85.114	29.411	28.398
<i>rosaceus</i>	0.902	-83.484	22.533	10.908
<i>ruberrimus</i>	0.957	-76.233	31.328	31.206
<i>saxicola</i>	0.977	-32.765	23.399	12.663
<i>semicinctus</i>	0.924	-19.182	25.266	6.961
<i>serranoides</i>	0.965	-51.013	29.350	18.965

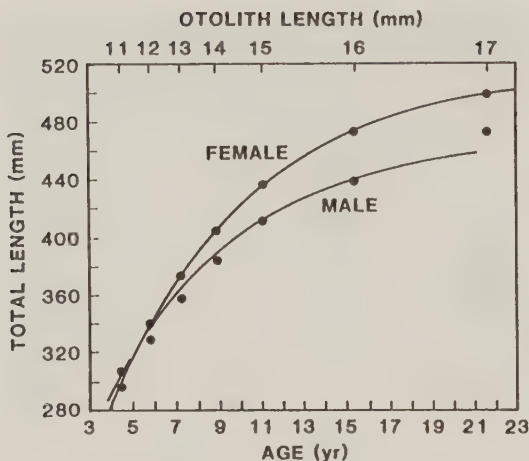


FIGURE 3.—Age-length curve for widow rockfish, *Sebastes entomelas* (from Lenarz 1987). The calculated total length from otolith length is overlaid on the curve to obtain an estimate of age.

should be used within well-defined limits. The scattergram (Fig. 2) with the mean and range of total length found at each 1 mm otolith length increment indicates the ranges within which these data are useful. Some problems in relating otolith length to age include the increased range of fish lengths at older ages and the observed thickening-instead of lengthening of otoliths in *Sebastes* (Boehlert 1985).

These results may be used to estimate total length from an otolith length as shown in the following example. If the otoliths are from fish of unknown sex, the regression statistics from Table 3 would be used to estimate fish length. If the otoliths are from fish of known sex, Table 2 would be consulted. If a species appears in Table 2, the regression statistics for the appropriate sex would be used to estimate fish length. If a species does not appear in Table 2, Table 3 (with regression statistics for males and females combined) would be used. For instance, to estimate fish length from otolith length (OL) for male *S. auriculatus*, the regression statistics from Table 3 are used. An otolith 10.0 mm long gives an estimated total length of

$$\begin{aligned} TL &= a + b (OL) \\ TL &= -53.032 + 33.159(10.0) \\ TL &= 279 \text{ mm.} \end{aligned}$$

Tables have been constructed with the regression statistics presented here. The table for each species (and sex, where appropriate) represents otolith lengths measured in millimeters and the correspond-

ing estimated total length. These tables are available on request from the author.

Acknowledgments

I wish to thank Sharon Moreland for assistance in measuring the otoliths, and David Woodbury and Carol Reilly for editing the data and running the computer programs. The reviews by George Boehlert, Bill Barss, and an anonymous reviewer were very helpful.

Literature Cited

- AINLEY, D. G., D. W. ANDERSON, AND P. R. KELLY.
1981. Feeding ecology of marine cormorants in southwestern North America. *Condor* 83:120-131.
- BARSUKOV, V. V.
1981. A brief review of the subfamily Sebastinae. *J. Ichthyol.* 2(1):1-26. (Engl. Transl. *Vopr. Ikhtiol.*)
- BOEHLERT, G. W.
1985. Using objective criteria and multiple regression models for age determination in fishes. *Fish. Bull., U.S.* 83:103-117.
- BOEHLERT, G. W., AND R. F. KAPPENMAN.
1980. Variation of growth with latitude in two species of rockfish (*Sebastes pinniger* and *S. diploproa*) from the northeast Pacific Ocean. *Mar. Ecol. Prog. Ser.* 3:1-10.
- CHEN, L.-C.
1971. Systematics, variation, distribution, and biology of rockfishes of the subgenus *Sebastomus* (Pisces, Scorpaenidae, *Sebastes*). *Bull. Scripps Inst. Oceanogr. Univ. Calif.* 18, 115 p.
- FITCH, J. E.
1972. Fish remains, primarily otoliths, from a coastal Indian midden (SLO-2) at Diablo Cove, San Luis Obispo County, California. *San Luis Obispo Cty. Archaeol. Soc. Occas. Pap. No. 7*:101-120.
- FITCH, J. E., AND R. L. BROWNELL, JR.
1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. *J. Fish. Res. Board Can.* 25:2561-2574.
- KIMURA, D. K., R. R. MANDAPAT, AND S. L. OXFORD.
1979. Method, validity, and variability in the age determination of yellowtail rockfish (*Sebastes flavidus*), using otoliths. *J. Fish. Res. Board Can.* 36:377-383.
- KLEINBAUM, D. G., AND L. L. KUPPER.
1978. Applied regression analysis and other multivariable methods. Duxbury Press, North Scituate, MA., 556 p.
- LENARZ, W. H.
1987. Aging and growth of widow rockfish. In W. H. Lenarz and D. R. Gunderson (editors), *Widow rockfish: Proceedings of a Workshop*, Tiburon, California, December 11-12, 1980, p. 31-35. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 48.
- LOVE, M. S., AND W. V. WESTPHAL.
1981. Growth, reproduction, and food habits of olive rockfish, *Sebastes serranoides*, off central California. *Fish. Bull., U.S.* 79:533-545.
- MILLER, D. J., AND J. J. GEIBEL.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. *Calif. Dep. Fish Game, Fish Bull.* 158, 137 p.

- MORROW, J. E.
1979. Preliminary keys to otoliths of some adult fishes of the Gulf of Alaska, Bering Sea, and Beaufort Sea. U.S. Dep. Commer., NOAA Tech. Rep. NMFS Circ. 420, 32 p.
- SEN, A. R.
1984. Sampling commercial rockfish landings in California. U.S. Dep. Commer., NOAA Tech. Memo. NOAA-TM-NMFS-SWFC-45, 95 p.
- SHAW, W., AND C. P. ARCHIBALD.
1981. Length and age data of rockfishes collected from B.C. coastal waters during 1977, 1978, and 1979. Can. Data Rep. Fish. Aquat. Sci. 289, 119 p.
- SIX, L. D., AND H. F. HORTON.
1977. Analysis of age determination methods for yellowtail rockfish, canary rockfish, and black rockfish off Oregon. Fish. Bull., U.S. 75:405-414.
- TREACY, S. D., AND T. W. CRAWFORD.
1981. Retrieval of otoliths and statoliths from gastrointestinal contents and scats of marine mammals. J. Wildl. Manage. 45:990-993.
- WESTRHEIM, S. J., AND W. R. HARLING.
1975. Age-length relationships for 26 scorpaenids in the northeast Pacific Ocean. Can. Fish. Mar. Serv. Tech. Rep. 565, 12 p.
- WILKINS, M. E.
1980. Size composition, age composition, and growth of chilipepper, *Sebastes goodei*, and bocaccio, *S. paucispinis*, from the 1977 rockfish survey. Mar. Fish. Rev. 42(3-4):48-53.
- WYLLIE ECHEVERRIA, T.
1986. Sexual dimorphism in four species of rockfish genus *Sebastes* (Scorpaenidae). Environ. Biol. Fish. 15:181-190.
- ZAITLAN, J. A.
1986. Geographical variation in the life history of *Sebastes chrysomelas*. M.A. Thesis, San Francisco State Univ., San Francisco, CA, 87 p.

TINA WYLLIE ECHEVERRIA

Southwest Fisheries Center Tiburon Laboratory
National Marine Fisheries Service, NOAA
3150 Paradise Drive, Tiburon, CA 94920

THIRTY-FOUR SPECIES OF CALIFORNIA ROCKFISHES: MATURITY AND SEASONALITY OF REPRODUCTION

TINA WYLLIE ECHEVERRIA¹

ABSTRACT

The viviparous rockfishes (*Sebastes* spp.) differ among species in age and size at maturity, and in the timing of peak spermatogenesis, fertilization, and larval extrusion. Age at 50% maturity ranges from 2 years in *S. jordani* to 9 years in *S. diploproa*. Within species, males usually mature either at the same age and size as females or at a younger age and smaller size. Rockfishes have two major seasons of larval extrusion, winter (November-March) or spring (April-July). The reproductive season for a particular species will fall within one of the major seasons throughout its geographic range. Within the major season, annual variations in the peak month of larval extrusion was observed for individual species. A long reproductive season and variations in the annual timing of that season are evidence of plasticity in the reproductive biology of rockfishes.

Reproductive development at the cellular level was compared with the coincident changes in the gross morphology of the gonads. The resulting description of the developmental sequences of the testes and ovaries enables the determination of maturity stage in the field.

Reproductive parameters such as age and size at maturity have been shown to be adaptive characteristics and are responsive to external pressures. For example, reduced population size due to fishing pressure may be associated with increased growth rate, reduced age at maturity, decreased fecundity, or a change in the gonadal index (Adams 1980; Gunderson 1980). For haddock, *Melanogrammus aeglefinus*, age at maturity was reduced and growth rates increased as the fishery increased (Templeman and Bishop 1979; Beacham 1983). Clupeoids shifted spawning location or time, and reduced age at maturity (Murphy 1977; Blaxter and Hunter 1982). A study of depleted populations of Pacific mackerel, *Scomber japonicus*, suggested a direct relationship between population size and age at maturity (Parrish and MacCall 1978). Pacific halibut, *Hippoglossus stenolepis*, stocks also showed reduced age at maturity and increased growth rates with reduced populations (Schmitt and Skud 1978). Age at maturity may thus be a useful indicator of heavy fishing mortality.

Rockfishes exhibit a variety of life history patterns, but only a few species have been studied in detail (Chen 1971; Miller and Geibel 1973; Patten 1973; Moulton 1977; Larson 1980; Love and Westphal 1981; McClure 1982). Previously, the most comprehensive work on the maturity of rockfishes was

by Phillips (1964) and Westrheim (1975). Phillips (1964) sampled market landings from northern and central California over several years. For each of the 10 species he investigated, maturity was reported for the sexes combined, and ages at maturity were derived from back-calculated von Bertalanffy growth curves. Westrheim (1975) summarized 10 years of data gathered on trawl-caught fish off British Columbia and the Gulf of Alaska, for which he reported on size at maturity and reproductive seasonality. Most of the fish in his study are commercially important species for British Columbia and, except for three species, do not occur off California.

There are some difficulties in assessing maturity stages and reproductive seasonality in rockfishes. One problem is the use of external morphology of gonads to determine maturity stages. Some researchers have questioned the accuracy with which immature fish can be distinguished from resting, mature fish during the nonreproductive months (Gunderson et al. 1980; Rosenthal et al. 1982). Also, the potential reproductive season may be protracted and the peak time of reproduction may shift within this season, so that short-term studies may be misleading. Thus, reported variation in length and age at maturity between studies could be the result of uncertainty in maturity-stage determinations.

In this study, I clarify the determination of sexual maturity stages, determine age and size at sexual maturity, and survey the reproductive seasonality for 34 species of rockfishes from the waters off

¹Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

northern and central California, from Port San Luis to Crescent City. I outline the reproductive patterns among species and annual variation within species.

MATERIALS AND METHODS

Data for this study were collected between July 1977 and July 1982 from three sources: 1) a coast-wide survey for adult rockfish made in July and August 1977 (Gunderson and Lenarz 1980); 2) an ongoing cooperative program, initiated in 1977 by the California Department of Fish and Game and the National Marine Fisheries Service, to sample the commercial (Sen 1984) and sport rockfish landings in northern and central California; and 3) a 1980 expansion of the cooperative program, to include data on gonad condition, prey items, seasonal fluctuation of interstitial fat, and gonad volumes. Additional collections were taken during cooperative survey trips with the National Marine Fisheries Service, Southwest Fisheries Center, and the California Department of Fish and Game. Fish were collected to supplement rarely sampled species and subadults that were not well represented in the three surveys.

Information on maturity was gathered primarily for seven species of commercial and sportfishing importance. Data for 27 additional species are presented, but these were inadequately sampled for statistical treatment of the data (Table 1). For each fish sampled from 1977 to 1982 the species, sex, and total length (mm) was determined in the field and otoliths were collected for age determination. The viscera from each of the 16,444 fish sampled from 1980 to 1982 were removed, preserved in 10% buffered formalin, and sent to the laboratory for analysis. In the laboratory the sex was verified and the maturity stage of the gonads was determined based on the criteria defined in this paper. Total length was measured from the most anterior part of the jaw to the dorsal tip of the caudal fin. When necessary, total lengths were converted to fork length to compare this study with others (Echeverria and Lenarz 1984).

Ages were determined for all fish investigated in this study. Most estimates of age were made from the surface of whole otoliths immersed in 70% ethyl alcohol, under a dissecting microscope at 12 $\times$. Standard techniques for counting annuli on whole otoliths were followed (Kimura et al. 1979; Shaw and Archibald 1981). Certain species such as *S. diploproa* required thin sectioning techniques for counting annuli (Beamish 1979). In some species it is difficult to determine what constitutes an annulus (Table 1), and consequently those ages have not been

validated. The "break-and-burn" method of age determination (Chilton and Beamish 1982) is useful and more accurate than surface ages when aging fish older than 16 years (Tagart 1984). Ages were not redetermined in this study because the age at maturity occurs before 16 years. Maximum ages, however, may be underestimated.

The gonad conditions described for males are immature, maturing, mature (peak spermatogenesis), spent, and resting. For females, they are immature, maturing, mature (fertilized), ripe (eyed larvae), recently spent, and resting (Lyubimova 1965; Westrheim 1975; Gunderson et al. 1980). Histological sections were examined to define seasonal maturation and the sections were analyzed based on the criteria established by Moser (1967b) for *S. paucispinis* and by Lisovenko (1970) on *S. alutus* for mature fish. The development of germ cells into spermatozoa or mature oocytes was examined to determine the developmental sequence leading to maturity. Cellular development was compared with the external morphology (Westrheim 1975; Gunderson et al. 1980) to understand clearly the developmental sequence and to aid in the interpretation of maturity stages in the field. Gonads were subsampled from fish in all maturity stages. Whole gonads were sectioned and stained with hematoxylin. Histological sections were examined from 519 testes and 708 ovaries from 30 species (Table 1). Egg diameters were routinely measured from histological sections and checked against whole eggs using an ocular micrometer.

To determine age and size at maturity and reproductive seasonality, the approximate age and size when 50% and 100% of the males and females were mature were estimated for each species. For those commercial species for which large samples were available, I checked the accuracy of the rough maturity estimates by applying the method of Gunderson et al. (1980). These authors used the logistic model

$$P_x = \frac{1}{1 + e^{ax+b}}$$

where P_x = proportion mature at size x , and a and b are constants, to estimate the length at 50% maturity for a sample. I applied a transformation of this equation

$$\ln \frac{1}{P_x} - 1 = ax + b$$

to obtain estimates of a and b for size and age by

TABLE 1.—Sample characteristics used to determine age and size at maturity and seasonality for *Sebastes* from central California.

Species of <i>Sebastes</i> (common name)	Sampled		Total number		Histology	
	Age (yr)	Size (cm TL)	Immature (N)	Mature (N)	Males (N)	Females (N)
<i>alutus</i>						
(Pacific ocean perch)	5-16	26-54	2	83	2	2
<i>auriculatus</i> (brown rockfish)	1-19	10-52	140	281	16	20
<i>aurora</i> (aurora rockfish)	5-19	20-39	2	92	—	1
<i>babcocki</i>						
(redbanded rockfish)	3-24	23-66	23	137	1	2
<i>caninus</i> (gopher rockfish) ¹	2-14	9-37	14	99	3	3
<i>caurinus</i> (copper rockfish)	3-20	19-57	49	276	17	14
<i>chlorostictus</i>						
(greenspotted rockfish) ²	3-33	16-57	83	236	17	18
<i>chrysomelas</i>						
(black and yellow rockfish) ¹	1-12	9-38	19	189	—	1
<i>constellatus</i> (starry rockfish) ²	2-15	12-44	58	152	6	4
<i>crameri</i>						
(darkblotched rockfish)	2-24	12-56	42	365	6	27
<i>diploproa</i>						
(splitnose rockfish)	3-27	13-40	44	266	1	3
<i>elongatus</i>						
(greenstriped rockfish)	2-21	13-31	33	215	16	12
<i>entomelas</i> (widow rockfish) ³	3-31	26-58	182	2,285	25	28
<i>flavidus</i> (yellowtail rockfish) ³	4-32	25-56	548	1,762	30	40
<i>goodei</i> (chilipepper) ³	2-21	21-59	256	2,312	35	34
<i>helvomaculatus</i>						
(rosethorn rockfish) ^{1,2}	5-11	20-28	7	25	1	1
<i>hopkinsi</i>						
(squarespot rockfish) ¹	2-13	12-30	15	45	—	—
<i>jordani</i> (shortbelly rockfish) ¹	1-12	12-20	47	635	9	9
<i>levis</i> (cowcod) ^{1,2}	2-22	24-90	17	24	—	—
<i>maliger</i> (quillback rockfish) ¹	6-15	22-44	4	45	3	—
<i>melanops</i> (black rockfish) ³	2-21	25-61	265	469	29	46
<i>melanostomus</i>						
(blackgill rockfish)	6-27	25-56	17	109	1	2
<i>miniatus</i> (vermillion rockfish)	5-30	30-67	12	96	7	2
<i>mystinus</i> (blue rockfish) ³	2-23	21-49	263	1,297	16	48
<i>nebulosus</i> (china rockfish) ¹	1-17	8-44	13	56	4	3
<i>ovalis</i> (speckled rockfish) ^{1,2}	3-15	23-49	6	101	—	2
<i>paucispinis</i>						
(bocaccio rockfish) ³	2-26	32-83	1,402	2,404	170	245
<i>pinniger</i> (canary rockfish) ³	3-26	22-69	564	641	61	105
<i>rosaceus</i> (rosy rockfish) ²	3-12	14-32	26	167	30	17
<i>ruberrimus</i>						
(yelloweye rockfish) ²	3-30	25-69	46	86	8	6
<i>rubrivinctus</i> (flag rockfish) ¹	4-18	19-45	4	38	3	—
<i>rufus</i> (bank rockfish) ²	2-24	19-54	25	137	—	—
<i>saxicola</i> (stripetail rockfish)	2-17	14-38	11	102	—	5
<i>serranoides</i> (olive rockfish) ¹	4-19	23-54	47	187	3	9

¹Denotes species not sampled every month for determination of seasonality²Denotes difficult to interpret otoliths for age determination.³Denotes species of major importance in the sport or commercial fisheries of California.

standard linear regression. These estimates of a and b were then used to calculate estimates of size or age (x) at 50% maturity ($P = 0.5$). This was done for all species with a sample of 10 specimens or more for each length or age. Where adequate data existed, P_{50} for a species was calculated by year and area to investigate possible yearly or geographic variation.

Reproductive stages for mature individuals were summarized by month, and the percentages of in-

dividuals at each reproductive stage were used to determine principal months of spermatogenesis (approximates mating), fertilization, and larval extrusion for each species. Seasonality was described only approximately for those species that were not present in all months sampled (Table 1).

Reproductive months for mature females were determined and the percentage containing eyed larvae was noted. Data from 1981 through 1985 were tabulated to compare annual variability in the

reproductive months and/or the principal month of parturition.

RESULTS

Moser (1967b) described the seasonal changes in gonads of mature *S. paucispinis* and should be consulted for details of morphology. In this study a general description of all maturity stages is included with emphasis on the immature gonad and the transitional stages, which are difficult to interpret. The transitional stages are 1) the determination of the first reproductive year, particularly in species with small maximum size; 2) the prespawning testis during spermatogenesis compared with the spawning and postspawning testis when spermatogenesis is completed and mating is in progress or just completed; 3) the unfertilized egg stage compared with the recently fertilized egg; and 4) the nonreproductive season, compared with the beginning of vitellogenesis or spermatogenesis when the gonads are beginning to mature. A comparison of external morphology with the histological sections indicates that the same sequence of spermatogenesis/vitellogenesis, mating, ovulation, fertilization, and larval extrusion is followed for each species in this study. There were not sufficient samples of all 31 species to discern what developmental variations might exist on the cellular level (Table 1).

Developmental Sequence of Ovaries

The germ cells in ovaries are clustered in oogonial nests, which are present throughout the year in varying numbers. The ovary of an immature rockfish (Gonad Stage 1) consists primarily of oogonial nests with oocytes <0.14 mm in diameter. The ovarian wall is translucent and thin (approximately 0.1 mm thick). Externally the ovary appears translucent with a tiny egg mass (Table 2).

Approaching the first year of maturity (Gonad Stage 2), the ovary is filled with oogonial nests, follicles begin to form around maturing oocytes, and the ovarian wall is translucent and thin. There is no evidence of the resorption and reorganization seen in spent ovaries. Externally the ovary appears pink through the thin wall, and eggs about 0.2 mm in diameter are visible.

As the reproductive season approaches (Gonad Stage 3) eggs are produced by the oogonial nests and vitellogenesis begins, resulting in eggs enlarging from 0.2 to 0.5 mm in diameter. Follicles form around the maturing eggs, a capillary network develops throughout the ovary, and the ovarian wall begins to thicken from 0.3 to 0.5 mm. Externally the ovary appears either white or yellow and firmly packed with eggs in grapelike clusters. The eggs expand during this stage, so that during maturation

TABLE 2.—Reproductive development at the cellular and external morphology level for ovaries of *Sebastes* species.

Gonad stage	Cellular morphology	External morphology
1. Immature	Oogonial nests with oocytes <0.14 mm. Ovarian wall (OW) 0.1 mm thick.	Small and translucent to pink. Ovarian wall (OW) thin.
2. First year maturity	Oocytes <0.2 mm. No evidence of resorption.	Pink with visible eggs. No black pigmentation. OW thin.
3. Vitellogenesis	Mature oocytes 0.2-0.5 mm in diameter within follicles. OW 0.3-0.4 mm thick.	Yellow or white opaque eggs in grapelike clusters. OW thickening.
4. Fertilization	Oocytes 0.9 mm. Yolk globule disintegration, ovulation, fertilization.	Large clear eggs free in ovarian cavity, but enveloped by a network of capillaries.
5. Eyed larvae (parturition)	Larvae developed within chorion with eyes pigmented black or yellow.	Large, soft, gray. Ovary breaks easily, and is filled with eggs and fluid.
6. Spawning	Oocytes 0.08-0.64 mm in diameter. Resorption of blood vessels, atretic oocytes, and residual larvae. Collapsed egg cases. OW 0.5-1.0 mm thick.	Flaccid, reddish-purple, or grayish from residual larvae. OW thick and tough.
7. Resting	Resorption and reorganization. Proliferation of oogonial nests. OW 0.5-0.9 mm thick.	Firm, gray to pink. Tiny black dots indicate residual larvae. OW thick, tough, and loose from eggs.

the ovary swells in size. The eggs remain opaque, and held within a follicle.

Fertilized eggs (Gonad Stage 4) are about 0.9 mm in diameter and have shed their follicles, and the yolk globules have disintegrated. Externally the eggs appear translucent yellow or white and are no longer held in tight grapelike clusters. They are held within an elaborate capillary network, not totally free within the ovary, though they are no longer held within a follicle.

Development of the embryos continues for about a month (Moser 1967a) until they develop pigmented eyes (Gonad Stage 5) and become ready for release. The pigmented eyes are usually black except in *S. ruberrimus* where they are yellow. Externally the ovary is gray (from the pigmented eyes) and very fragile. It breaks easily when handled and usually some larvae are prematurely extruded when the adult is captured.

After normal release of the larvae (Gonad Stage 6), the ovary consists primarily of an elaborate vascular system, larvae that were not extruded, and a few eggs which failed to develop (atretic oocytes). Externally it appears very mushy and reddish gray, with an opaque and flaccid ovarian wall.

Resorption and reorganization of the ovary (Gonad Stage 7) occur until vitellogenesis begins (Gonad Stage 3) again. During the months of reorganization (Figs. 1-7) there is evidence of residual larvae, eggs, and capillaries being resorbed, and a proliferation of oogonial nests producing eggs for the next reproductive season. The ovarian wall is between 0.5 and 0.9 mm thick. Externally the ovary is compact and loosely encased by an opaque wall. During resorption the ovary changes from reddish

brown to grayish brown. When vitellogenesis begins again (Gonad Stage 3) the ovary appears yellow or white. There are usually a few pigmented eyes being resorbed through Gonad Stage 3 from the previous year's brood.

The principal external characteristic of an immature ovary entering the first reproductive season is the wall, which is thin (0.1 mm) and translucent. There are also no residual pigmented eyes in the ovary. A spent and maturing ovary from a mature fish usually contains remnants of resorbed larvae (evidenced as black dots) encased by a thick, opaque ovarian wall (0.5 to 0.9 mm).

Developmental Sequence for Testes

It is often difficult to distinguish an immature from a resting testis in rockfish because the presence of sperm in the testis is not necessarily an indication of the fish's maturity. Understanding the developmental sequence of spermatogenesis can help to identify the reproductive stage any time of year (Table 3).

Histological examination shows that the immature testis (Gonad Stage 1) consists of germ cells, primary spermatogonia, and secondary spermatogonia which lend a whitish color at the periphery. Externally the testis is threadlike and translucent, often with a hint of white from the developing spermatogonia.

Spermatogenesis begins at the periphery of the testis and moves centripetally, filling the lumen, the efferent ducts, and finally the sperm duct. A male approaching the first year of maturity (Gonad Stage

TABLE 3.—Reproductive development at the cellular and external morphology level for testes of *Sebastes* species.

Gonad stage	Cellular morphology	External morphology
1. Immature	Germ cells, primary and secondary spermatogonia.	Small, threadlike; transparent to white at periphery.
2. First year maturity	Spermatozoan cysts throughout testis. No residual sperm in tubules or ducts.	Small, ribbonlike, and white. No evidence of sperm in central duct (translucent).
3. Spermatogenesis	Large spermatozoan cysts throughout testis with spermatozoa in lumen.	Milky white and swollen, sperm throughout testis in cross section.
4. Spawning	Sperm duct and lumen filled with spermatozoa. Spermatogenesis ceases at periphery.	Large, soft, white; sperm flows freely when cut. Center of testis white, periphery becoming translucent.
6. Recently spawned	Abundance of germ cells at periphery. Resorption of sperm by tubular boundary cells.	Center is white in cross section, with the periphery becoming firm and darker.
7. Resting	Reorganization of testis. Germ cells line spermatogenic tubules.	Firm, compact, and vaguely triangular. Color dark gray/brown.

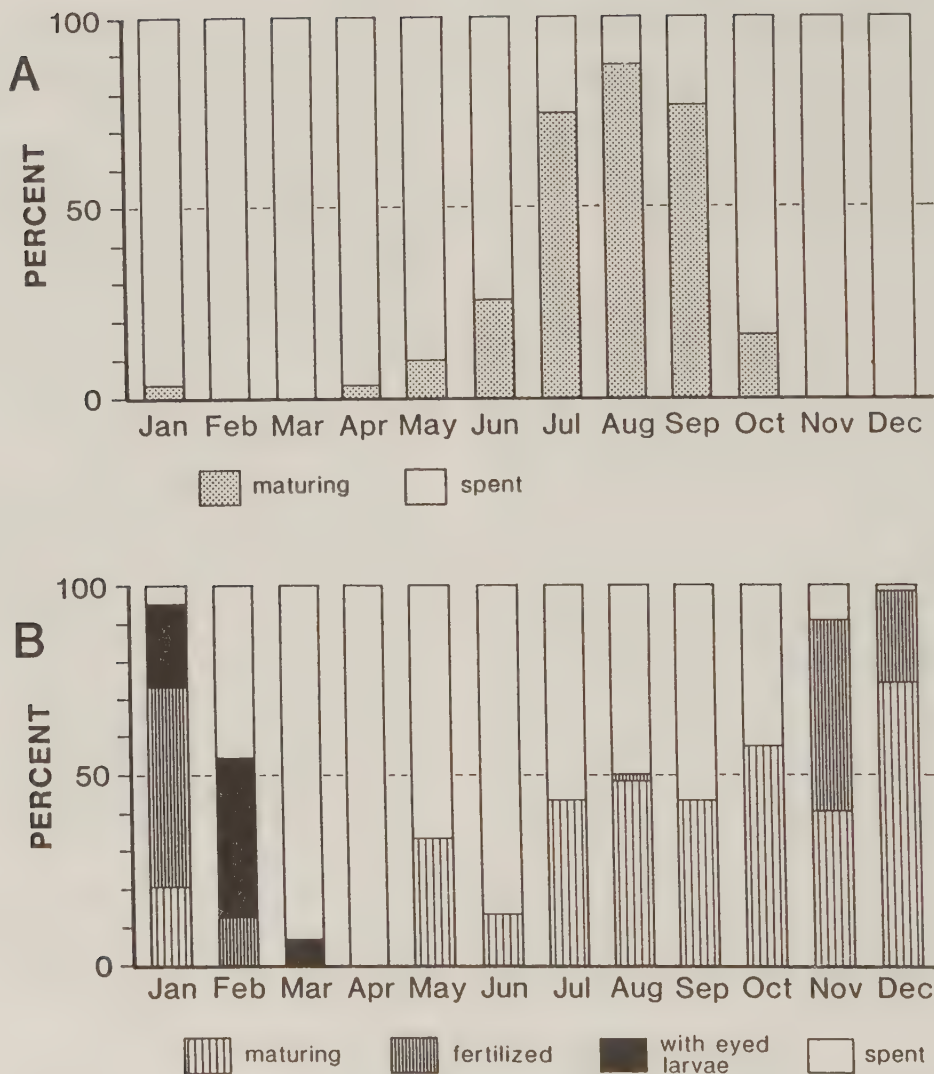


FIGURE 1.—A. Reproductive seasonality of mature males of *Sebastes entomelas* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. entomelas* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

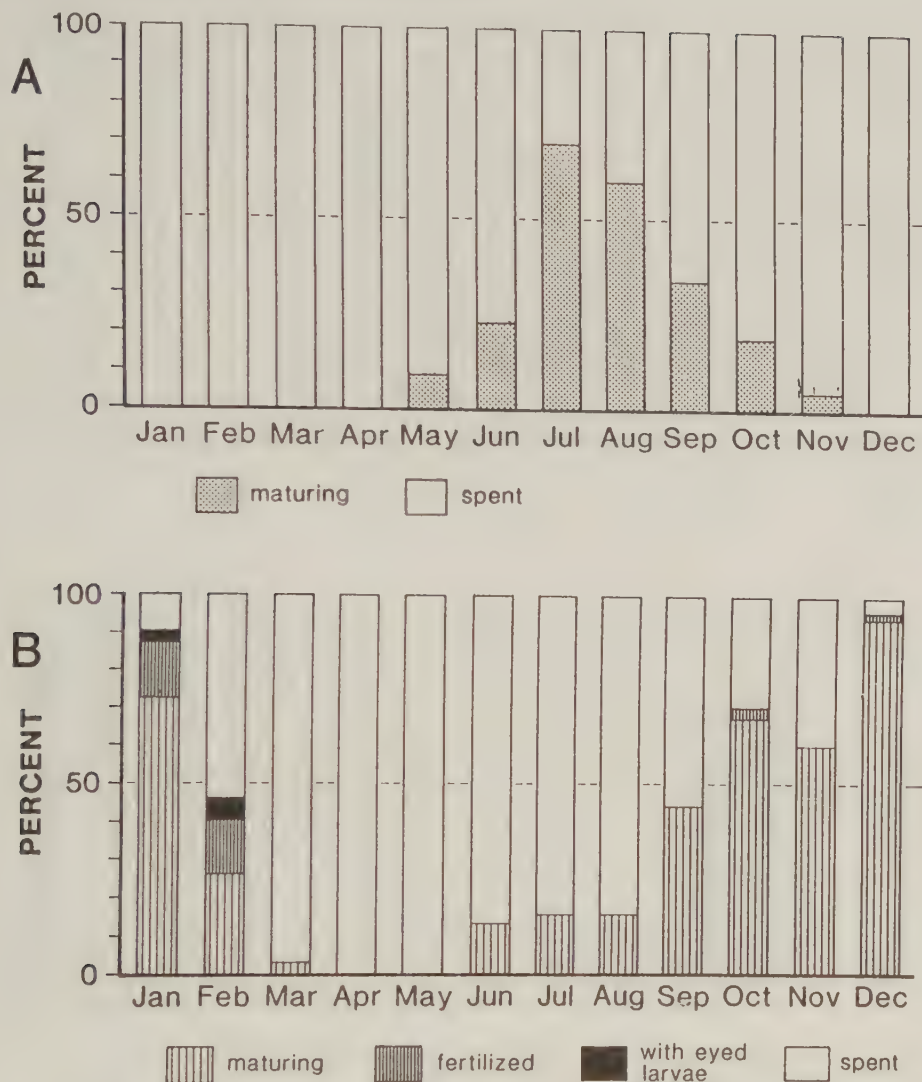


FIGURE 2.—A. Reproductive seasonality of mature males of *Sebastes flavidus* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. flavidus* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

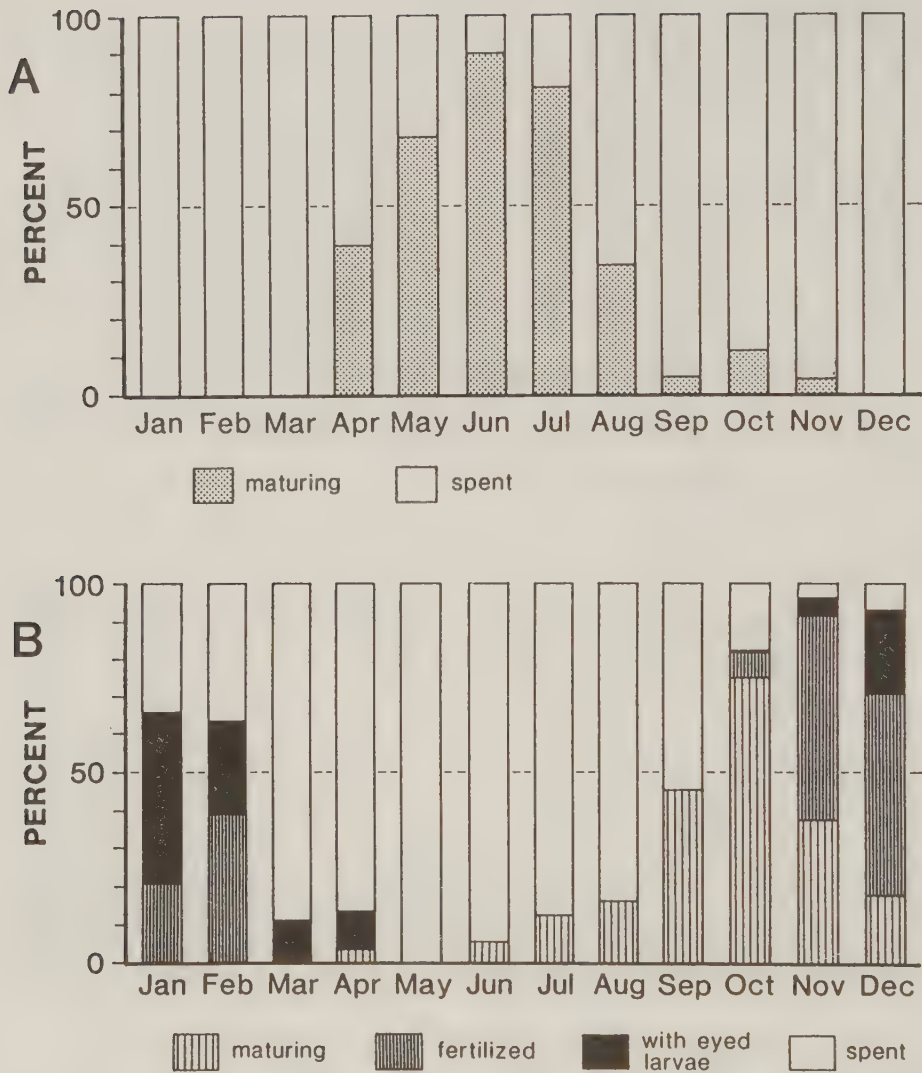


FIGURE 3.—A. Reproductive seasonality of mature males of *Sebastes goodei* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. goodei* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

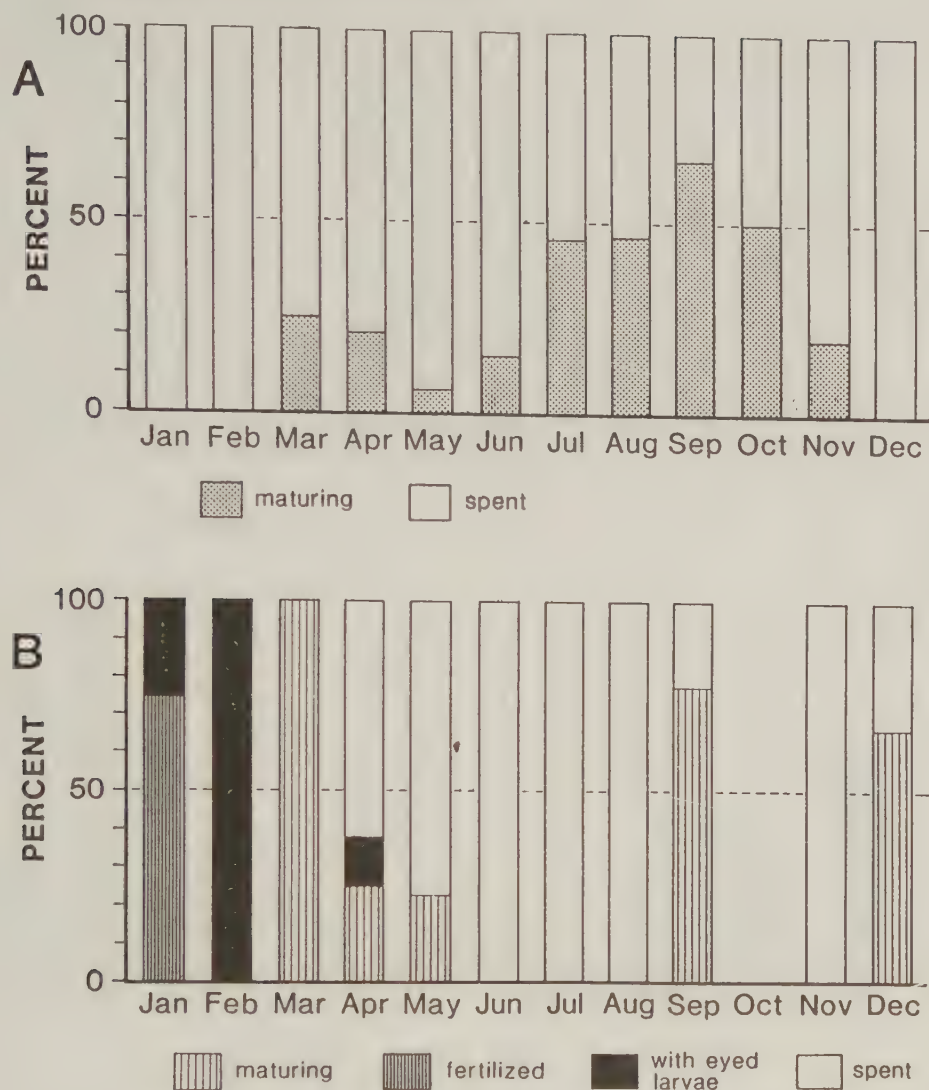


FIGURE 4.—A. Reproductive seasonality of mature males of *Sebastes melanops* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. melanops* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

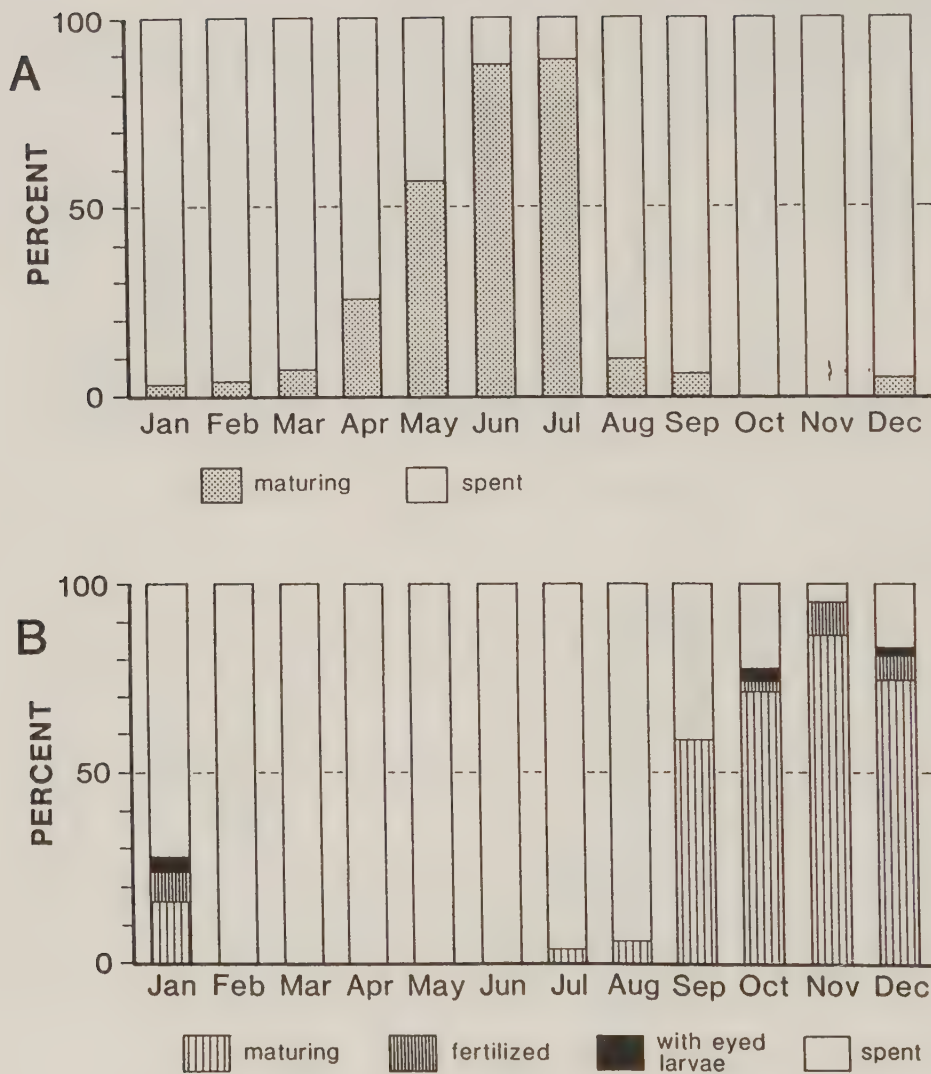


FIGURE 5.—A. Reproductive seasonality of mature males of *Sebastes mystinus* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. mystinus* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

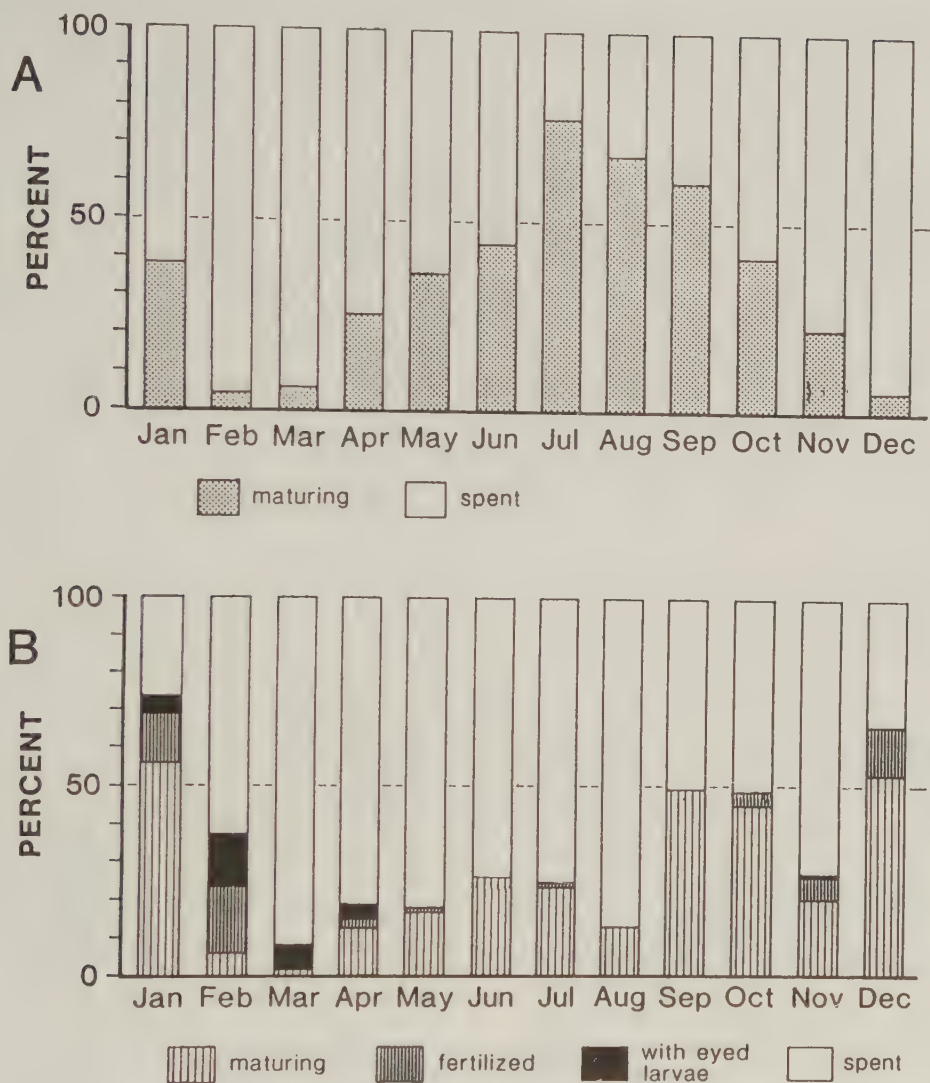


FIGURE 6.—A. Reproductive seasonality of mature males of *Sebastes paucispinis* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. paucispinis* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

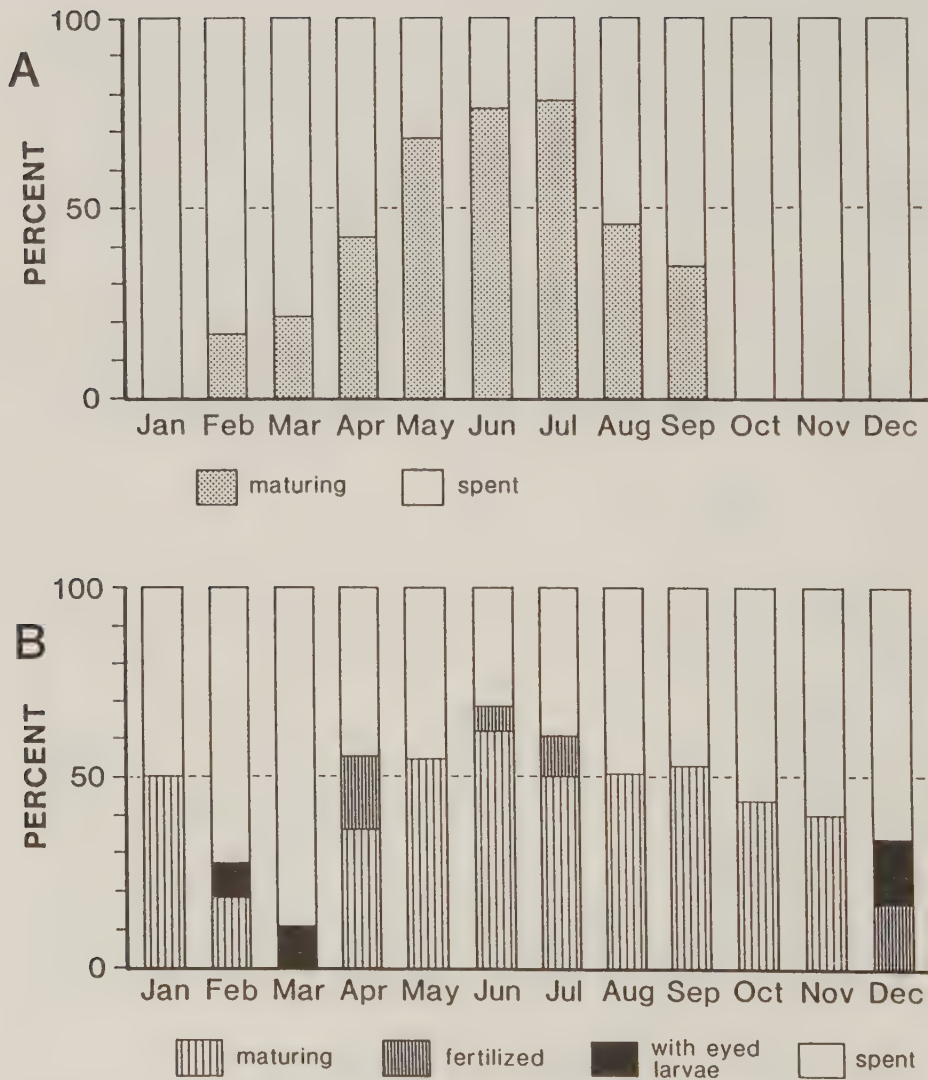


FIGURE 7.—A. Reproductive seasonality of mature males of *Sebastes pinniger* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. pinniger* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

2) has spermatogonial cysts developing throughout the testis. There is no sign of spermatozoa in the sperm duct. Externally, the testes appear slightly swollen and white; in cross section they are translucent in the center because of the absence of sperm in the sperm duct.

In a maturing male (Gonad Stage 3) spermatozoa appear throughout the testis in spermatozoan cysts. The sperm duct often contains remnants of residual sperm from the previous reproductive season. In a cross section the testis is swollen and whitish at the periphery and brownish off-white in the center because of the presence of residual sperm in the sperm duct.

As the reproductive season approaches (Gonad Stage 4) the spermatozoan cysts burst open, releasing spermatozoa into the efferent ducts and the sperm duct. Externally the testis is large, soft, and very white, sperm flows freely when the testis is pressed or cut. During the reproductive season spermatogenesis has ceased and the spermatozoa have moved from the periphery towards the sperm duct so that the periphery becomes hard and discolored. The central area may be swollen with sperm.

At the end of the reproductive season (Gonad Stage 7), the testis undergoes resorption and reorganization, wherein smooth muscle cells, connective tissue, and scattered residual spermatozoa, constituting cellular detritus, are evident in the histological sections. At the periphery, a new generation of germ cells reorganizes along the spermatogenic tubules. Externally the testis is a compact, irregular triangular shape that appears gray or brown.

An understanding of the developmental sequence on the cellular level aids in the interpretation of gonad stage in the field. The four, difficult to interpret, transitional stages can be clarified: 1) The first reproductive year is indicated by a white periphery (sperm) and an absence of sperm in the center of a cross section of testis, a thin ovarian wall and no residual pigmented eyes in ovaries. 2) The center of the prespawned testis is firm and a dark cream color (residual sperm); the periphery is white and swollen with sperm. The postspawned testis usually shows signs of white fluid (sperm) in the sperm duct and is firm and a dark cream color at the periphery. 3) Unfertilized eggs are opaque yellow or white held tightly in grapelike clusters while fertilized eggs are a translucent yellow or white and the outer eggs can be separated from each other. 4) Vitellogenesis is indicated by a deep yellow color and swelling of the eggs so that the ovarian wall fits tightly around the eggs; spermatogenesis is in-

dicated by a softening and swelling of the testis and a whitening at the periphery.

Reproductive Maturity and Seasonality

Maturity was observed over a broad age and size range within species throughout the years sampled. The age and size at first maturity, 50% maturity and 100% maturity were estimated for males and females of each species (Table 4). Males reached 50% maturity either at the same or younger age than females. Size at 50% maturity is generally similar or somewhat smaller for males than for females of the same species. The standard linear regressions were run on the transformed logistic for the seven principal species occurring in this study, resulting in similar estimates of age at 50% maturity for *S. entomelas*, *S. flavidus*, *S. goodei*, *S. melanops*, *S. mystinus*, *S. paucispinis*, and *S. pinniger* (Table 5), and similar, if not exact, sizes at 50% maturity as estimates derived from the raw data. Maturity for species without sufficient data for statistical treatment are estimated from the raw data.

The reproductive season in *Sebastes* can be long with larval extrusion (parturition) seen in females of some species for up to 9 months (Table 6). From all the data collected between 1977 and 1984 a summary of principal month of spermatogenesis, fertilization, and parturition was determined for 32 species (Table 7). A span of 1 to 5 months between peak spermatogenesis and fertilization is seen. The time, when males ripen and mate, is not dependent upon the eggs being fully mature. The time between fertilization and parturition is usually about 1 month (Moser 1967a).

Reproductive seasonality for the principal species sampled is displayed graphically in Figures 1-7. Seasonality histograms are available, upon request, for most species investigated. The general trend in the seasonality of *Sebastes* is a prolonged reproductive period for each maturity stage. This trend is seen in the seven most abundant species sampled (Figs. 1-7). Spermatogenesis (Gonad Stage 3) occurs over 3 to 5 months before the testes are fully ripe (Gonad Stage 4). The timing of mating is estimated from the appearance of testes swollen with sperm. At least part of the male population is ready for mating for a period of 2 to 4 months. In females, generally, fertilized eggs (Gonad Stage 4) are found 1 to 3 months after mating. Eyed larvae (Gonad Stage 5) appear from 1 to 4 months after fertilized eggs were observed and were present in the sampled population for 3 to 6 months, usually with a

TABLE 4.—Estimated age and size at 1st, 50% and 100% maturity for given in cm

Species of <i>Sebastes</i>	Male						Female					
	1st		50%		100%		1st		50%		100%	
	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL
<i>alutus</i>	—	—	5	28	7	32	7	26	7	26	7	32
<i>auriculatus</i>	3	26	5	31	10	38	3	26	5	31	10	38
<i>aurora</i>	5	28	—	—	5	28	5	28	—	—	5	28
<i>babcocki</i>	3	27	4	31	5	36	3	32	4	34	6	41
<i>carnatus</i>	4	17	4	17	5	21	4	17	4	17	5	21
<i>caurinus</i>	3	30	4	32	7	40	5	31	6	34	8	41
<i>chlorostictus</i>	4	25	6	27	12	38	5	26	6	28	9	34
<i>chrysomelas</i>	3	14	3	16	5	20	3	14	3	15	5	19
<i>constellatus</i>	6	28	7	30	12	36	5	23	6	27	9	34
<i>crameri</i>	3	25	4	27	7	36	3	24	4	27	6	34
<i>diploproa</i>	7	20	9	22	10	29	6	18	7	19	9	23
<i>elongatus</i>	7	23	7	23	10	27	5	18	7	23	10	27
<i>entomelas</i> ¹	3	31	5	36	8	41	3	29	5	37	8	40
<i>flavidus</i> ¹	4	30	6	35	11	43	4	27	7	36	11	42
<i>goodei</i> ¹	2	26	3	31	7	38	2	29	3	34	6	39
<i>helvomaculatus</i>	7	22	7	22	10	27	5	20	8	23	10	27
<i>hopkinsi</i>	4	15	5	16	5	17	5	17	5	18	7	21

¹Denotes samples from 1980-82 study only.

peak month of larval extrusion. The external appearance of individual ovaries indicates that larvae are in the eyed stage and ready for release throughout the ovary.

The total number of mature females observed during the reproductive months, and the percentage containing eyed larvae is presented for three commercially important species (Figs. 8-10). For the years 1981-85, variations in the months of parturition and/or the peak month is seen. *Sebastes entomelas* (Fig. 8) showed an annual variation in the months of parturition but not in the peak months (January-February). The peak month for *S. goodei* (Fig. 9) varied from December to February, and in *S. paucispinis* (Fig. 10) from December to March. A variation in which months larval extrusion occurs is seen in all three species. Chi-square tests showed the percentages to be dependent upon year and month. Therefore, there is a relationship between the percent-number of mature females with eyed larvae seen in a particular month, and reproductive year.

DISCUSSION

The reproductive biology of *Sebastes* follows the sequence of spermatogenesis, vitellogenesis, mating, ovulation, fertilization, and larval extrusion (Moser 1967b). As in other viviparous fishes (Turner 1947), sperm can apparently survive within the ovary for many months. In *S. mentella*, ovulation and the activation of sperm coincide with a change in pH

(Sorokin 1967). The histological evaluation of the gonads in *Sebastes* of northern California confirms that spermatogenesis is generally completed and mating occurs before the completion of vitellogenesis. The length of time males are fully ripe can be up to 2 months in various species, and the delay between the time males are fully ripe and fertilization (sometimes up to 4 months) indicates that mating does not coincide with fully mature ova (Figs. 1-7). Testes are observed in decreasing degrees of ripeness after spermatogenesis has ceased. This indicates that one mating does not void the testes; males may mate more than once per season. Ovulation in teleosts is regulated by steroids and prostaglandins, which in turn are influenced to some degree by temperature, pheromones, or spatial/temporal cues (Stacey 1984). The presence of sperm in the ovaries of *Sebastes* does not trigger final oocyte maturation and ovulation; therefore, ovulation is probably influenced by environmental conditions. Thus knowing which conditions influence ovulation is necessary to determine some of the factors contributing to a successful reproductive year, as measured by the percent mature females with eyed larvae.

The costs of reproduction for females include the development of a highly vascular network throughout the ovaries, the nourishing of developing embryos (Boehlert and Yoklavich 1984), and the metabolism of waste products from the embryos (Moser 1967a). The ovaries must accommodate the added gonadal weight and volume until larval extrusion.

Sebastes from northern and central California collected 1977-82. Lengths total length (TL).

Species of <i>Sebastes</i>	Male						Female					
	1st		50%		100%		1st		50%		100%	
	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL
<i>jordani</i>	1	12	2	14	5	20	2	12	3	14	4	19
<i>levis</i>	4	32	4	32	4	32	4	32	4	32	5	37
<i>maliger</i>	4	22	4	22	7	31	6	26	6	26	7	28
<i>melanops</i> ¹	3	25	6	36	10	43	5	30	7	41	11	48
<i>melanostomus</i>	6	29	7	33	10	39	7	30	8	35	9	36
<i>miniatus</i>	5	35	5	38	8	43	5	37	5	37	9	46
<i>mystinus</i> ¹	4	22	5	27	9	32	5	22	6	29	11	35
<i>nebulosus</i>	3	26	4	27	6	30	3	26	4	27	6	30
<i>ovalis</i>	4	28	4	28	5	30	4	28	4	28	5	29
<i>paucispinis</i> ¹	3	32	3	42	7	55	3	36	4	48	8	60
<i>pinniger</i> ¹	4	28	7	40	9	45	4	27	9	44	13	54
<i>rosaceus</i>	4	16	6	20	8	25	4	15	6	20	8	25
<i>ruberrimus</i>	6	36	7	40	8	46	6	36	7	40	8	46
<i>rubrivinctus</i>	5	29	5	30	6	32	5	29	8	34	10	38
<i>rufus</i>	—	27	3	31	4	36	2	32	3	34	4	41
<i>saxicola</i>	3	15	3	16	4	17	2	17	2	17	3	18
<i>serranoides</i>	4	32	5	33	8	38	4	32	5	35	8	39

TABLE 5.—Standard linear regression used to estimate age (yr) and size (cm) at 50% maturity for males (M) and females (F) in seven species of *Sebastes*. Slope and y-intercept were estimated from the equation $\ln \frac{1}{P_x} - 1 = ax + b$. r = correlation coefficient, N = number of ages or sizes used in the regressions; each N represents at least 10 observations per age or size.

Species of <i>Sebastes</i>	Sex	Variable	y-intercept	Slope	50% maturity	r	N
<i>entomelas</i>	M	age	4.5598	-1.0006	5	-0.9588	6
		size	10.1042	-0.3162	33	-0.7649	11
	F	age	5.4800	-0.7982	5	-0.9647	5
		size	28.4810	-0.7810	37	-0.9667	4
<i>flavidus</i>	M	age	2.9748	-0.4994	6	-0.9577	10
		size	13.7834	-0.3964	35	-0.9718	14
	F	age	5.3731	-0.7757	7	-0.9541	9
		size	15.7482	-0.4331	36	-0.9723	13
<i>goodei</i>	M	age	1.1620	-0.4093	3	-0.9263	9
		size	7.7618	-0.3044	31	-0.8730	10
	F	age	3.7624	-1.1129	3	-0.9775	6
		size	12.2400	-0.3740	34	-0.9650	15
<i>melanops</i>	M	age	4.3841	-0.8011	6	-0.9769	6
		size	13.7147	-0.3814	36	-0.9411	6
	F	age	5.0627	-0.7149	7	-0.9760	8
		size	11.0749	-0.2720	41	-0.9520	16
<i>mystinus</i>	M	age	1.3482	-0.3669	5	-0.8530	10
		size	4.3885	-0.2049	27	-0.6778	11
	F	age	5.0097	-0.8022	6	-0.9680	9
		size	9.5090	-0.3368	29	-0.9218	17
<i>paucispinis</i>	M	age	1.7138	-0.6677	3	-0.9431	8
		size	10.7040	-0.2564	42	-0.9196	16
	F	age	3.5175	-0.8232	4	-0.9232	7
		size	13.7028	-0.2876	48	-0.9565	20
<i>pinniger</i>	M	age	3.7804	-0.5845	7	-0.9710	9
		size	11.2047	-0.2837	40	-0.9500	16
	F	age	5.1221	-0.5897	9	-0.9800	11
		size	11.5621	-0.5897	44	-0.9460	15

TABLE 6.—Months of parturition for species of *Sebastes* that occur in the northeastern Pacific Ocean. All available data are listed by area (results of this study in parentheses).

Species of <i>Sebastes</i>	Gulf of Alaska	British Columbia	Washington	Oregon	North-Central California	Southern California
<i>aleutianus</i>		Apr. ¹		May ²		
<i>alutus</i>	May ³ , Apr.-May ¹	Mar. ³	Mar. ⁴	Jan.-Apr. ²	(Jan.-Mar.)	
<i>auriculatus</i>				June ⁵ , May ⁶	(Dec.-Jan.; May-July), May ⁷	
<i>aurea</i>		>June ¹			(Mar.-May)	
<i>babcocki</i>		Apr. ¹		Apr. ²	(May)	
<i>borealis</i>		Apr. ¹				
<i>brevispinis</i>		>May ¹				
<i>carnatus</i>					(Mar.-May), May ⁷	
<i>caurinus</i>			Mar. ⁸ , Apr. ^{6,9,5}		(Feb.)	
<i>chlorostictus</i>				Apr. ²	(Apr.-Sept.)	Apr.-July ¹⁰ , July ¹¹
<i>chrysomelas</i>					(Feb.-Mar.), Jan.-May ⁷	
<i>constellatus</i>					(Apr.-May)	Mar. + May ^{10,11}
<i>crameri</i>	<June ¹	Feb. ¹		Feb.-Mar. ²	(Nov.-Mar.), Nov.-Mar. ⁷	
<i>diploproa</i>		July ¹	July ⁶	Apr.-May ¹²	(Jan.-Sept.), Feb.-July ¹³	
<i>elongatus</i>		>June ¹		Apr.-May ¹²	(May-July)	
<i>ensifer</i>						Feb. + May ¹⁰
<i>entomelas</i>		Apr. ¹		Jan. ^{2,14}	(Dec.-Apr.), Nov.-Mar. ¹³	
<i>eos</i>						Apr.-June ¹¹
<i>flavidus</i>		Mar. ¹	Jan.-Apr. ⁴	Jan.-Mar. ²	(Jan.-July), Nov.-Mar. ¹³	
<i>goodei</i>					(Nov.-June), Nov.-Mar. ¹³	Oct.-Mar. ¹¹
<i>helvomaculatus</i>	>May ¹	>May ¹			(May-June)	
<i>hopkinsi</i>					(Feb.-Mar.)	
<i>jordani</i>				Feb. ²	(Feb.-Apr.), Nov.-Mar. ¹³	
<i>lentiginosus</i>						Mar. ¹⁰
<i>levis</i>					(Dec.-Feb.)	Dec.-Jan. ¹¹
<i>maliger</i>	May-July ¹⁵	Apr. ^{1,16} , May ⁵			(Apr.-July)	
<i>melanops</i>		Jan. ¹⁷ , <Apr. ¹		Jan. ¹⁷	(Jan.-May)	
<i>melanostomus</i>					(Feb.-Apr.)	
<i>miniatus</i>					(Sept.) Nov. ¹¹ , Nov.-Mar. ¹³	Nov. ¹¹
<i>mystinus</i>					(Nov.-Jan.), Nov.-Jan. ¹⁸ , Jan.-Mar. ¹⁹	
<i>nebulosus</i>					(Jan.-June), Jan. ²⁰	
<i>nigrocinctus</i>		May ¹				
<i>ovalis</i>					(May)	Jan.-May ¹¹
<i>paucispinis</i>		<Feb. ¹	Jan.-Apr. ⁴	Jan.-Feb. ²	(Jan.-May), Nov.-Mar. ¹¹	Oct.-Mar. ¹¹
<i>pinniger</i>		>Feb. ¹		Dec.-Apr. ²	(Dec.-Mar.), Nov.-Mar. ¹¹	
<i>proriger</i>				Apr.-July ²	(July-Aug.)	
<i>reedi</i>		May ¹		Feb.-May ¹⁵		
<i>rosaceus</i>					(Apr.-July)	Mar. + May ^{10,11}
<i>ruberrimus</i>	June-Aug. ¹⁵	May ¹	July ⁶	Mar.-Apr. ²	(Apr.-June)	
<i>rubrivinctus</i>				Apr.-May ¹²		
<i>rufus</i>		May ¹		Apr.-May ¹²	(July)	Mar.-June ¹⁰
<i>saxicola</i>		Feb. ¹			(Dec.-May)	
<i>serranoides</i>				Feb. ²	(Jan.-Mar.), Nov.-Mar. ¹³	
<i>simulator</i>					(Jan.-Mar.)	Jan. ¹⁶
<i>umbrosus</i>						Feb.-Mar. ¹⁰
<i>wilsoni</i>		June ¹				Apr. ¹⁰
<i>zacentrus</i>	>May ¹	July ¹		Mar.-July ² , Apr.-May ¹²	(May-June)	

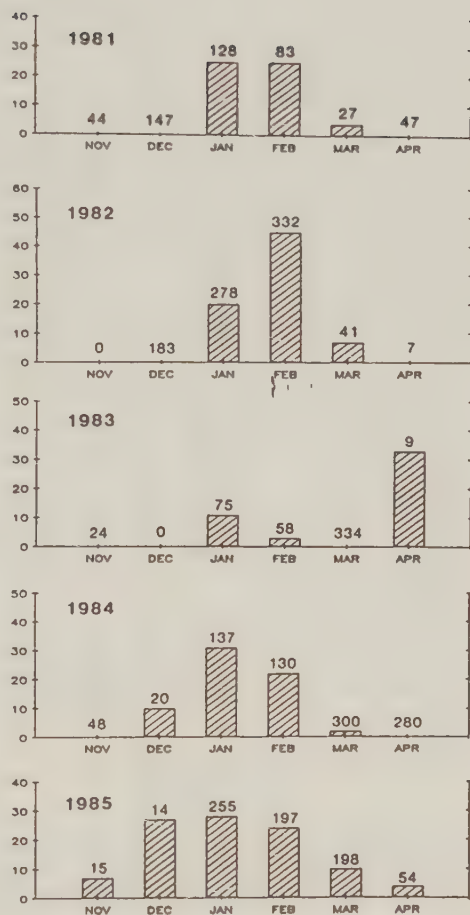
¹Westheim 1975.²W. H. Barss, Oregon Department of Fish and Wildlife, Marine Science Drive, Newport, OR 97365, pers. commun. 1985.³Lyubimova 1965.⁴Gunderson et al. 1980.⁵Washington et al. 1978.⁶DeLacy et al. 1964.⁷Larson 1980.⁸Patten 1973.⁹Moulton 1977.¹⁰Chen 1971.¹¹Moser 1967a.¹²Hiltz 1962.¹³Phillips 1964.¹⁴Barss and Echeverria 1987.¹⁵Rosenthal et al. 1981.¹⁶Love and Westphal 1981.¹⁷Dunn and Hiltz 1969.¹⁸Wales 1952.¹⁹Miller and Geibel 1973.²⁰Burge and Schultz 1973.

TABLE 7.—Reproductive seasonality for *Sebastes* from central California collected 1977-84. Listed by taxonomic order (Barsukov 1981).

Species of <i>Sebastes</i>	Principal month(s) of		
	spermato-genesis	fertilization	parturi-tion
<i>melanostomus</i>	Nov.	Feb.	Feb.
<i>aurora</i>	Apr.	?	Apr.
<i>ruberrimus</i>	Dec.	Apr.	June
<i>chrysomelas</i>	?	Jan.	Feb.
<i>carinatus</i>	Dec.	?	Mar.
<i>nebulosus</i>	?	Jan.	Jan.
<i>auriculatus</i>	May	May	June
<i>caurinus</i>	Dec.	Jan.	Feb.
<i>maliger</i>	Dec.-Jan.	Apr.	Apr.
<i>elongatus</i>	?	Apr.	May
<i>babcocki</i>	Jan.	?	May
<i>saxicola</i>	?	Dec.	Jan.
<i>diploproa</i>	June	June	July
<i>crameri</i>	?	Dec.	Jan.
<i>alutus</i>	Sept.-Oct.	?	Mar.
<i>pinniger</i>	Oct.	Dec.	Dec.
<i>miniatus</i>	July	?	Sept.
<i>levis</i>	Sept.-Oct.	Oct.	Dec.
<i>rosaceus</i>	May	May	June
<i>constellatus</i>	Dec.	Feb.	Apr.
<i>chlorostictus</i>	Feb.	Apr.	May
<i>goodei</i>	Oct.	Dec.	Jan.
<i>jordani</i>	Nov.	Jan.	Feb.
<i>paucispinis</i>	Oct.	Dec.	Feb.
<i>ovalis</i>	Nov.	?	May
<i>rufus</i>	Nov.	Nov.	Feb.
<i>hopkinsi</i>	Dec.	Feb.	Mar.
<i>entomelas</i>	Oct.	Jan.	Feb.
<i>mystinus</i>	Aug.	Jan.	Jan.
<i>melanops</i>	Oct.	Jan.	Feb.
<i>flavivus</i>	Sept.	Jan.	Feb.
<i>serranoides</i>	Nov.	Jan.	Feb.

Females are exposed to changing environmental factors from year to year, so flexibility in the timing of their greatest reproductive involvement may be advantageous. The apparent flexibility of the period between mating and larval extrusion may be a mechanism to optimize reproductive success. A long and variable period of larval extrusion is exhibited by the rockfish group (Figs. 8-10). The evidence of two spawnings per season have been reported for *S. paucispinis* (Moser 1967a), *S. ovalis*, and *S. constellatus* (MacGregor 1970). Multiple broods are indicated by the presence of eyed larvae undergoing resorption in the ovary concurrently with vitellogenic eggs at least 0.4 mm in diameter. During the years and throughout the area of this study, evidence of multiple broods was rare: only one *S. paucispinis* gonad showed evidence of a multiple brood. Moser's (1967b) detailed description of the histology of multiple broods indicates the development and extrusion of a second brood follows within 2 months of the

PERCENT MATURE FEMALES WITH EYED-LARVAE

*Sebastes entomelas*FIGURE 8.—Percent of mature female *Sebastes entomelas* containing eyed larvae for the reproductive months during 1981-85. Total number of mature females observed are indicated over bars.

first. In this study, two distinct seasons of larval extrusion, December and June, were noticed in *S. auriculatus* sampled from a limited area (Pt. Reyes-Half Moon Bay) (Table 6) in north-central California. The entire reproductive sequence in *Sebastes* seems to reflect a plasticity for reproduction that may enable the individual to respond adaptively to environmental factors.

The consequences of the reproductive biology in *Sebastes* include the absence of strong spawning pulses, the possibility of multiple mating of males, and flexibility in the timing of fertilization. Apparently mating is not restricted to a short period

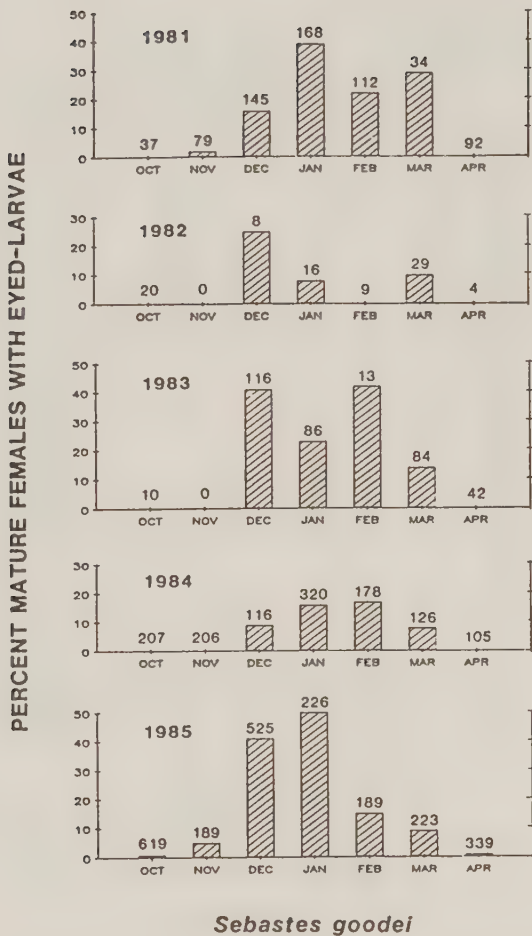


FIGURE 9.—Percent of mature female *Sebastes goodei* containing eyed larvae for the reproductive months during 1981-85. Total number of mature females observed are indicated over bars.

of time and elaborate displays to induce ovulation are not necessary. It is not surprising, therefore, to find so little information regarding mating behavior in the most speciose and populous group of fishes in north-central California (Helvey 1982).

Ages and sizes at maturity from this study generally agree with findings in the literature, but sometimes exhibit large discrepancies (Table 8). The variability has possible sources: differences in age determination techniques, length measurements, identification of the immature gonad stage, or sampling at times of the year when it is difficult to distinguish immature from resting fish. Previous studies on maturity often focused on adult popula-

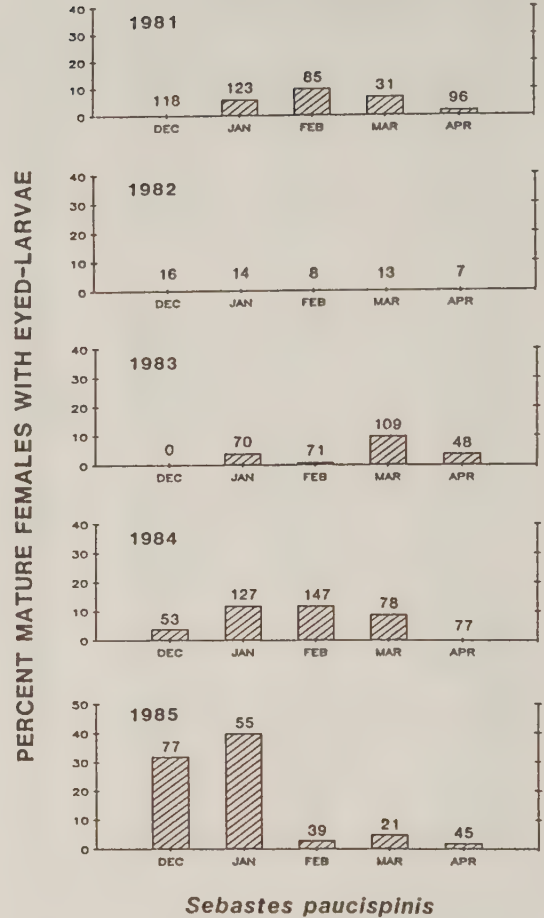


FIGURE 10.—Percent of mature female *Sebastes paucispinis* containing eyed larvae for the reproductive months during 1981-85. Total number of mature females observed are indicated over bars.

tions or were based on samples taken only during summer, when most species are not in reproductive condition (Westrheim 1975; Gunderson et al. 1980; Rosenthal et al. 1981, 1982). The differentiation of an immature gonad stage versus mature "resting" gonads is most difficult and subject to error during the nonreproductive months.

Age and size at 50% maturity by area and year were calculated for *S. flavidus*, *S. goodei*, and *S. paucispinis* (Table 9). Age and size at maturity did not differ geographically but did vary between years. Age varies up to 1 year and size varies up to 3 cm. Apparently, there is some variability in age and size at maturity within a population between years. The normal range of variation of size and age

TABLE 8.—Age and size at 50% maturity for male (M) and female (F) *Sebastes* by area. All lengths are converted to fork length for comparison (Echeverria and Lenarz 1984).

Species of <i>Sebastes</i>	Alaska	British Columbia	Washington	Oregon	California	this study
<i>auriculatus</i>						
M			4 yr, 23 cm FL ¹			5 yr, 31 cm FL
F			4 yr, 25 cm FL			5 yr, 31 cm FL
<i>entomelas</i>						
M		37 cm FL ²		4 yr, 33 cm FL ³	{ 4 yr, 29 cm FL ⁴	5 yr, 32 cm FL
F		38 cm FL		7 yr, 38 cm FL		5 yr, 36 cm FL
<i>flavids</i>						
M	{ 11-15 yr ⁵ 41-45 cm FL	40 cm FL, 40.5 cm FL ^{2,6}			5 yr, 31 cm FL ⁴	6 yr, 32 cm FL
F		42 cm FL, 45 cm FL				7 yr, 33 cm FL
<i>goodei</i>						
M				26 cm FL ⁶	4 yr, 28 cm FL ⁴	3 yr, 29 cm FL
F				37 cm FL	4 yr, 30 cm FL	3 yr, 32 cm FL
<i>melanops</i>						
M	10-13 yr, 40-42 cm FL ⁵		3 yr, 21 cm FL ⁷	5 yr ⁸		6 yr, 35 cm FL
F	9-12 yr, 39-42 cm FL		3-4 yr, 33 cm FL	6 yr		7 yr, 40 cm FL
<i>mystinus</i>						
M				3 yr ⁸	6-7 yr ⁹	5 yr, 26 cm FL
F				4 yr	6 yr	6 yr, 28 cm FL
<i>paucispinis</i>						
M		<57 cm FL ²	5 yr, 45 cm FL ⁷		{ 4 yr ⁴	3 yr, 39 cm FL
F		<62 cm FL	6 yr, 48 cm FL		{ 37 cm FL	4 yr, 45 cm FL
<i>pinniger</i>						
M		41 cm FL ^{2,6}		12 yr, 39 cm FL ⁸	{ 5-6 yr ⁴	7 yr, 39 cm FL
F		48 cm FL		10 yr, 43 cm FL	{ 33 cm FL	9 yr, 43 cm FL

¹Washington et al. 1978; ²Westrheim 1975; ³Barss and Echeverria 1987; ⁴Phillips 1964; ⁵Rosenthal et al. 1982; ⁶Gunderson et al. 1980; ⁷Barker 1979; ⁸McClure 1982; ⁹Miller et al. 1967

at maturity should be determined before subtle shifts in these parameters are studied.

Later spawning in high latitude populations occurs in some teleosts as a response to temperature and photoperiod (Wootton 1984). The existence of geographical trends for spawning months can be determined for a species if data exist for the same months and years. Parturition occurred somewhat earlier in the southern end of the range of *S.*

maliger, *S. ruberrimus*, and *S. entomelas*. *Sebastes maliger* extruded larvae between May and July off Alaska (Rosenthal et al. 1981, 1982) and between April and July off California during 1982. *Sebastes ruberrimus* extruded larvae between June and August off Alaska (Rosenthal et al. 1981, 1982) and between April and July off California during 1982. *Sebastes entomelas* extruded larvae in February off Oregon and in January off California in 1982 (Barss and Echeverria 1987) (Table 6). For species where comparable data exist, parturition is earlier in the southern end of the species range.

Reproductive seasonality can be classified into one of two broad seasons, early (winter) or late (spring-summer) (Phillips 1964), which seems to hold true throughout a species range (Table 6). The duration of larval extrusion varies from 1 to 9 months and is species-specific. Closely related species have similar seasons of parturition, but the peak month may differ (Table 7).

Data on parturition may be useful when investigating recruitment by estimating annual reproductive success. To predict year-class strength for species of *Sebastes*, it must be possible to identify species in the juvenile stages. Juvenile identifications have been described for 18 species of rockfish

TABLE 9.—Age and size of three *Sebastes* species at 50% maturity derived from linear regressions for males (M) and females (F) by area and by year for the area between Crescent City and Morro Bay.

Data base	Sex	<i>S. flavids</i>		<i>S. goodei</i>		<i>S. paucispinis</i>	
		yr	cm TL	yr	cm TL	yr	cm TL
North of Point Arena	M	—	—	4	—	3	43
	F	—	—	4	—	4	48
South of Point Arena	M	—	—	4	31	3	43
	F	—	—	4	33	4	47
April 1980-March 1981	M	6	35	4	31	3	43
	F	7	37	4	34	4	48
April 1981-March 1982	M	7	38	5	33	3	42
	F	6	36	4	32	4	47
April 1980-March 1982	M	6	35	4	31	3	43
	F	7	36	4	34	4	48

that occur off California (Moser and Ahlstrom 1978; Richardson and Laroche 1979; Laroche and Richardson 1980, 1981; Anderson 1983); the difficulties of differentiating between similar species are evident in these studies. Knowledge of the principal month of parturition may be a useful tool when identifying species in the age 0 population. Principal month of parturition would have to be documented for the year that recruitment is investigated.

Life history parameters that are interrelated, such as growth, maturity, and fecundity, can be influenced by external conditions, such as temperature, prey abundance, and predation (Stearns and Crandall 1984). The manner in which they can be affected is species-specific and may change in a predictable manner. Observed changes that coincide with reduced population sizes include increase in growth rates (Templeman and Bishop 1979), decrease in age at maturity (Murphy 1977; Parrish and MacCall 1978; Schmitt and Skud 1978; Templeman and Bishop 1979), and decrease in size at maturity (Alm 1959; Pitt 1975). Stearns and Crandall (1984) proposed that changes in age and/or size at maturity are determined by genetic as well as environmental factors, so that populations will respond in a predictable manner. A shift in either the age or size at maturity in *Sebastes* may be an indication of a change in population densities. In order to detect any population changes, age and size at maturity for species should be determined yearly and within a well-defined geographic area. Fish of the estimated age and size at first maturity should be included—sampling from market fish tends to yield only mature fish. Ages should be determined from the same fish that are sampled for maturity.

Fecundity in poikilotherms is generally related to size; changes in growth rates and size at maturity will affect fecundity. Fecundity often relates more to body size in short-lived species and to available energy in long-lived species (Ware 1980). Fecundity increases with size in at least some species of *Sebastes* (Phillips 1964), but annual reproductive success may be linked to available energy. Gonad volumes of female *S. flavidus* were reported for 1981 (Guillemot et al. 1985) and compared with volumes measured during the El Niño winter of 1983-84 (Lenarz and Wyllie Echeverria 1986); this comparison showed reduced gonad volumes in *S. flavidus* for the 1983 reproductive season. Whether the decreased gonad volume was due to egg size or number was not determined.

Shifts in age and/or size at maturity may occur in species that have a multigenerational, late-maturing population. In his studies of flatfish populations,

Roff (1982) predicted that size at maturity would be primarily influenced by size-dependent mortality and that changes in size at maturity would occur in species where growth to a minimal size is more adaptive than early reproduction. Changes in age at maturity will more likely occur in species that mature early. Changes in size, rather than age, at maturity would most likely occur in *Sebastes* subjected to overfishing or long-term environmental stress.

General changes in life history parameters may be predictable according to a species' position on the r - K selection continuum. Increased fishing mortality resulting in decreased populations may affect life history parameters by increasing growth rates, reducing age at first maturity, increasing fecundity at age (Adams 1980; Gunderson 1980), and reducing variability in the gene pool by reducing the number of spawning groups in the more K -selected species (Leaman and Beamish 1984). The reproductive strategy of *Sebastes* reflects more K -type characteristics, which include later maturity, slower growth rates, lower individual fecundity, or some degree of parental care (Garrod and Horwood 1984). The K -type reproductive strategy enables a species to minimize the effects of a poor reproductive year (Roff 1984). A disadvantage for a heavily fished K -type species is the late age at maturity, as exists in *Sebastes*, so that the advantage of many reproductive seasons must be balanced against adult population size to obtain an allowable harvest.

The reproductive strategy of *Sebastes*, with multiple generations reproducing simultaneously and the plasticity of annual timing, results in a buffered system. The populations of exploited stocks of *Sebastes* should be able to recover from a single year of high mortality due either to poor recruitment or to adult mortality. However, overfished populations or long periods of poor recruitment could result in a reduced size at maturity and a corresponding reduced fecundity.

ACKNOWLEDGMENTS

Among the many people who contributed to this research, I wish to thank the biologists and seasonal samplers of the California Department of Fish and Game, the personnel who assisted me in the collection and processing of these samples, including but not limited to Lisa Andrade, Todd Anderson, Patrick Guillemot, Steven Pace, Dana Tryde, Mickey Singer, Stuart Running, Marianne McLean, Karen Novak, Sonia Linnik, Michael King, Sally Krenn, Lisa Natanson, Kathleen Mathews, Laura

Young, and Jerry Kwiecien. I wish to thank William H. Lenarz for support and guidance, S. J. Westheim and Ralph Larson for their insightful reviews, and Sandy Wyllie Echeverria and Rahel Fischer for editorial assistance.

LITERATURE CITED

- ADAMS, P. B.
1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fish. Bull.*, U.S. 78:1-12.
- ALM, G.
1959. Connection between maturity, size and age in fishes. *Inst. Freshwater Res. Drottningholm Rep.* 40, 145 p.
- ANDERSON, T. W.
1983. Identification and development of nearshore juvenile rockfishes (genus *Sebastes*) in central California kelp forests. M.A. Thesis, San Francisco State Univ., San Francisco, CA, 216 p.
- BARKER, M. W.
1979. Population and fishery dynamics of recreationally exploited marine bottomfish of northern Puget Sound. *Diss. Abstr. Int. B Sci. Eng.* 40(6):2497.
- BARSS, W. H., AND T. ECHEVERRIA.
1987. Mortality of widow rockfish (*Sebastes entomelas*) from the northeast Pacific 1977-1981. In W. H. Lenarz and D. R. Gunderson (editors), *Proceedings of the Widow Rockfish Workshop*, 11-12 December 1980, Tiburon, CA. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC 48:13-18.
- BARSUKOV, V. V.
1981. A brief review of the subfamily Sebastinae. *J. Ichthyol.* 21:1-26.
- BEACHAM, T. D.
1983. Variability in size and age at sexual maturity of haddock (*Melanogrammus aeglefinus*) on the Scotian Shelf in the northwest Atlantic. *Can. Tech. Rep. Fish. Aquat. Sci.* 1168, 33 p.
- BEAMISH, R. J.
1979. New information on the longevity of Pacific ocean perch (*Sebastes alutus*). *J. Fish. Res. Board Can.* 36:1395-1400.
- BLAXTER, J. H. S., AND J. R. HUNTER.
1982. The biology of the clupeoid fishes. *Adv. Mar. Biol.* 20:1-223.
- BOEHLERT, G. W., AND M. YOKLAVICH.
1984. Reproduction, embryonic energetics, and the maternal fetal relationship in the viviparous genus *Sebastes* (Pisces: Scorpaenidae). *Biol. Bull. (Woods Hole)* 167:354-370.
- BURGE, R. T., AND S. A. SCHULTZ.
1973. The marine environment in the vicinity of Diablo Cove with special reference to abalones and bony fishes. *Calif. Dep. Fish Game, Mar. Resour. Tech. Rep.* 19, 433 p.
- CHEN, L. C.
1971. Systematics, variation, distribution, and biology of the subgenus *Sebastes* (Pisces, Scorpaenidae, *Sebastes*). *Ru. Sci. Scripps Inst. Oceanogr.* 18, 115 p.
- CHILTON, D. E., AND R. J. BEAMISH.
1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. *Can. Spec. Publ. Fish. Aquat. Sci.* 60, 102 p.
- DELACY, A. C., C. R. HITZ, AND R. L. DRYFOOS.
1964. Maturation, gestation, and birth of rockfish (*Sebastes*) from Washington and adjacent waters. *Wash. Dep. Fish.*, *Fish. Res. Pap.* 2(3):51-67.
- DUNN, J. R., AND C. R. HITZ.
1969. Oceanic occurrence of black rockfish (*Sebastes melanops*) in the central north Pacific. *J. Fish. Res. Board Can.* 26:3094-3097.
- ECHEVERRIA, T., AND W. H. LENARZ.
1984. Conversions between total, fork, and standard lengths in 35 species of *Sebastes* from California. *Fish. Bull.*, U.S. 82:249-251.
- GARROD, D. J., AND J. W. HORWOOD.
1984. Reproductive strategies and the response to exploitation. In G. W. Potts and R. J. Wootton (editors), *Fish reproduction: strategies and tactics*, p. 367-384. Acad. Press, Lond.
- GUILLEMOT, P. J., R. J. LARSON, AND W. H. LENARZ.
1985. Seasonal cycles of fat and gonad volume in five species of northern California rockfish (Scorpaenidae; *Sebastes*). *Fish. Bull.*, U.S. 83:299-311.
- GUNDERSON, D. R.
1980. Using r -K selection theory to predict natural mortality. *Can. J. Fish. Aquat. Sci.* 37:2266-2271.
- GUNDERSON, D. R., P. CALLAHAN, AND B. GOINEY.
1980. Maturation and fecundity of four species of *Sebastes*. *Mar. Fish. Rev.* 42(3-4):74-79.
- GUNDERSON, D. R., AND W. H. LENARZ.
1980. Cooperative survey of rockfish and whiting resources off California, Washington, and Oregon, 1977: Introduction. *Mar. Fish. Rev.* 42(3-4):1.
- HELVEY, M.
1982. First observations of courtship behavior in rockfish, genus *Sebastes*. *Copeia* 1982:763-770.
- HITZ, C. R.
1962. Seasons of birth of rockfish (*Sebastes* spp.) in Oregon coastal waters. *Trans. Am. Fish. Soc.* 91:231-233.
- KIMURA, D. K., R. R. MANDAPAT, AND S. L. OXFORD.
1979. Method, validity, and variability in the age determination of yellowtail rockfish, *Sebastes flavidus*, using otoliths. *J. Fish. Res. Board Can.* 36:377-383.
- LAROCHE, W. A., AND S. L. RICHARDSON.
1980. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes flavidus* and *Sebastes melanops* (Scorpaenidae) off Oregon. *Fish. Bull.*, U.S. 77:901-924.
1981. Development of larvae and juveniles of the rockfishes *Sebastes entomelas* and *S. zacentrus* (family Scorpaenidae) and occurrence off Oregon, with notes on head spines, of *S. mystinus*, *S. flavidus*, and *S. melanops*. *Fish. Bull.*, U.S. 79:231-257.
- LARSON, R. J.
1980. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. *Ecol. Monogr.* 50:221-239.
- LEAMAN, B. M., AND R. J. BEAMISH.
1984. Ecological and management implications of longevity in some northeastern Pacific groundfishes. *Int. N. Pac. Fish. Comm. Bull.* 42:85-97.
- LENARZ, W. H., AND T. WYLLIE ECHEVERRIA.
1986. Comparison of visceral fat and gonadal fat volumes of yellowtail rockfish, *Sebastes flavidus*, during a normal year and a year of El Niño conditions. *Fish. Bull.*, U.S. 84:743-745.
- LISOVENKO, L. A.
1970. A study of spermatogenesis in Pacific rockfish *Sebastes alutus* (Gilbert) from the Gulf of Alaska. In Moiseev, P. A. (editor), *Soviet fisheries investigations in the northeastern Pacific*, Part V, p. 248-266. Israel Program Sci. Transl. Jerusalem.

- LOVE, M. S., AND W. V. WESTPHAL.
1981. Growth, reproduction, and food habits of olive rockfish, *Sebastes serranoides*, off central California. Fish. Bull., U.S. 79:533-545.
- LYUBIMOVA, T. G.
1965. Main stages in the life cycle of the rockfish *Sebastes alutus* (Gilbert) in the Gulf of Alaska. Tr. VNIRO 49:85-111.
- MACGREGOR, J. S.
1970. Fecundity, multiple spawning, and description of the gonads in *Sebastes*. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 596, 12 p.
- MCCLURE, R. E.
1982. Neretic reef fishes of central Oregon: aspects of life histories and the recreational fishery. M.S. Thesis, Oregon State Univ., Corvallis, OR, 94 p.
- MILLER, D. J., M. W. ODEMAR, AND D. W. GOTSHALL.
1967. Life history and catch analysis of the blue rockfish (*Sebastes mystinus*) off central California 1961-1965. Calif. Dep. Fish Game, MRO Ref. No. 67-14, 130 p.
- MILLER, D. J., AND J. J. GEIBEL.
1973. Summary of blue rockfish and lingcod life histories; a reef ecology study; and giant kelp, *Macrocystis pyrifera*, experiments in Monterey Bay, California. Calif. Dep. Fish Game, Fish Bull. 158, 137 p.
- MOSER, H. G.
1967a. Reproduction and development of *Sebastes paucispinis* and comparison with other rockfishes off southern California. Copeia 1967:773-797.
1967b. Seasonal histological changes in the gonads of *Sebastes paucispinis* (Ayres), an ovoviparous teleost (family Scorpaenidae). J. Morph. 123:329-351.
- MOSER, H. G., AND E. H. AHLSTROM.
1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Board Can. 35:981-996.
- MOULTON, L. L.
1977. An ecological analysis of fishes inhabiting the rocky nearshore regions of northern Puget Sound, Washington. Ph.D. Thesis, Univ. Washington, Seattle, 181 p.
- MURPHY, G. I.
1977. Clupeoids. In J. A. Gulland (editor), Fish population dynamics, Ch. 12, p. 283-308. John Wiley & Sons, Lond.
- PARRISH, R. H., AND A. D. MACCALL.
1978. Climatic variation and exploitation in the Pacific mackerel fishery. Calif. Dep. Fish Game, Fish Bull. 167, 110 p.
- PATTEN, C. G.
1973. Biological information on copper rockfish in Puget Sound, Washington. Trans. Am. Fish. Soc. 102:412-416.
- PHILLIPS, J. B.
1964. Life history studies on ten species of rockfish (genus *Sebastes*). Calif. Dep. Fish Game, Fish Bull. 126, 70 p.
- PITT, T. K.
1975. Changes in abundance and certain biological characteristics of Grand Bank American plaice, *Hippoglossoides platessoides*. J. Fish. Res. Board Can. 32:1383-1398.
- RICHARDSON, S. L., AND W. A. LAROCHE.
1979. Development and occurrence of larvae and juveniles of the rockfishes *Sebastes crameri*, *Sebastes pinniger*, and *Sebastes helvomaculatus* (Family: Scorpaenidae) off Oregon. Fish. Bull., U.S. 77:1-46.
- ROFF, D. A.
1982. Reproductive strategies in flatfish; a first synthesis. Can. J. Fish. Aquat. Sci. 39:1686-1698.
1984. The evolution of life history parameters in teleosts. Can. J. Fish. Aquat. Sci. 41:989-1000.
- ROSENTHAL, R. J., L. J. FIELD, AND D. MYER.
1981. Survey of nearshore bottomfish in the outside waters of southeastern Alaska. Prepared for Alaska Dep. Fish Game, Comm. Fish. Div., Juneau, AK, 91 p.
- ROSENTHAL, R. J., L. H. HALDORSON, L. J. FIELD, V. MORAN-O'CONNELL, M. G. LARIVIERA, J. UNDERWOOD, AND M. C. MURPHY.
1982. Inshore and shallow offshore bottomfish resources in the southeastern Gulf of Alaska (1981-1982). Prepared for Alaska Dep. Fish Game, Comm. Fish. Div., Juneau, AK, 166 p.
- SCHMITT, C. C., AND B. E. SKUD.
1978. Relation of fecundity to long-term changes in growth, abundance and recruitment. Int. Pac. Halibut Comm. Sci. Rep. 66, 31 p.
- SEN, A. R.
1984. Sampling commercial rockfish landings in California. U.S. Dep. Commer., NOAA-TM-NMFS-SWFC-45, 95 p.
- SHAW, W., AND C. P. ARCHIBALD.
1981. Length and age data of rockfishes collected from B.C. coastal waters during 1977, 1978, and 1979. Can. Data Rep. Fish. Aquat. Sci. 289, 119 p.
- SOROKIN, V. P.
1967. Some data on gametogenesis and sexual cycles of the Pacific Ocean Scorpaenidae. Tr. PINRO 20:304-315.
- STACEY, N. E.
1984. Control of the timing of ovulation by exogenous and endogenous factors. In G. W. Potts and R. J. Wootton (editors), Fish reproduction: strategies and tactics, p. 207-222. Acad. Press, Lond.
- STEARNS, S. C., AND R. E. CRANDALL.
1984. Plasticity for age and size at sexual maturity: a life-history response to unavoidable stress. In G. W. Potts and R. J. Wootton (editors), Fish reproduction: strategies and tactics, p. 13-33. Acad. Press, Lond.
- TAGART, J. V.
1984. Comparison of final ages assigned to a common set of Pacific ocean perch otoliths. Wash. Dep. Fish. Tech. Rep. 81, 36 p.
- TEMPLEMAN, W., AND C. A. BISHOP.
1979. Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, of St. Pierre bank. ICNAF Res. Bull. 14:77-83.
- TURNER, C. L.
1947. Viviparity in teleost fishes. Sci. Mon. 65:508-518.
- WALES, J. H.
1952. Life history of the blue rockfish *Sebastes mystinus*. Calif. Fish Game 38:485-498.
- WARE, D. H.
1980. Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. 37:1012-1024.
- WASHINGTON, P. M., R. GOWAN, AND D. H. ITO.
1978. A biological report on eight species of rockfish *Sebastes* spp. from Puget Sound, Washington. Northwest Alaska Fisheries Center, 50 p. [Processed rep.]
- WESTRHEIM, S. J.
1975. Reproduction, maturation, and identification of larvae of some *Sebastes* (Scorpaenidae) species in the northeast Pacific Ocean. J. Fish. Res. Board Can. 32:2399-2411.
- WOOTTON, R. J.
1984. Introduction: strategies and tactics in fish reproduction. In G. W. Potts and R. J. Wootton (editors), Fish reproduction: strategies and tactics, p. 1-12. Acad. Press, Lond.

DIEL HAUL-OUT PATTERNS AND SITE
FIDELITY OF HARBOR SEALS
(*PHOCA VITULINA RICHARDSI*)
ON SAN MIGUEL ISLAND,
CALIFORNIA, IN AUTUMN

PAMELA K. YOCHAM

BRENT S. STEWART

Sea World Research Institute,
Hubbs Marine Research Center,
1700 South Shores Rd.,
San Diego, California 92109

ROBERT L. DELONG

National Marine Mammal Laboratory, NMFS,
7600 Sand Point Way, N.E.,
Seattle, Washington 98115

DOUGLAS P. DEMASTER

Southwest Fisheries Center, NMFS,
8604 La Jolla Shores Drive,
La Jolla, California 92038

ABSTRACT

We studied the haul-out patterns and movements of harbor seals (*Phoca vitulina richardsi*) on San Miguel Island, California, from 23 October through 6 December 1982 by attaching a radio transmitter to each of 18 seals and monitoring their presence ashore with continuously scanning receivers. Seals hauled out at all hours although, on average, the largest proportion of tagged seals was ashore between 1300 and 1500 h. Median durations of haul-out bouts of individual seals ranged from 4.7 to 21.8 h; 81% of all haul-out bouts were less than 12 h and 3% were longer than 24 h. Eighty-one percent of the seals that were resighted at least twice used only the sites where they were tagged; two seals used two sites and one seal used three. Most seals were hauled out on fewer than 51% of the days sampled. On average, about 41% of tagged seals hauled out each day whereas an average of about 19% was hauled out during peak afternoon hours. Using telemetry data to correct a count of 412 seals made during an aerial survey, we estimated absolute abundance at about 2,168 seals; a modified Peterson mark-recapture model produced an estimate of about 1,445 seals.

Key words: pinnipedia, harbor seals, haul-out patterns, Southern California Channel Islands, San Miguel Island, radiotelemetry.

Numbers of harbor seals (*Phoca vitulina richardsi*) ashore on the Southern California Channel Islands vary seasonally, with the fewest ashore in December and the most ashore in late May and June, when seals are molting (Stewart 1981, 1984; Stewart and Yochem 1984). Using time-lapse photography, Stewart (1981, 1984) found that the number of seals ashore on San Miguel Island, at all seasons, was lowest in the morning, increased to a peak in early afternoon, and decreased towards sunset. Although tide height did not influence the timing of peak haul-out at most sites, where haul-out space was available during all tides, it did influence the number of seals ashore during afternoon peak hours (Stewart 1981).

We report here the results of a radiotelemetry study of harbor seals on San Miguel Island in autumn 1982. The objectives were to examine the frequency and duration of haul-out bouts, and the movements among haul-out sites of individual harbor seals; with that information and census data, we estimated the absolute number of harbor seals that were using San Miguel Island.

MATERIALS AND METHODS

We captured, using hoop nets, 18 seals at four sites on San Miguel Island (34°02'N, 120°22'W; Fig. 1) either by crawling to within several meters of

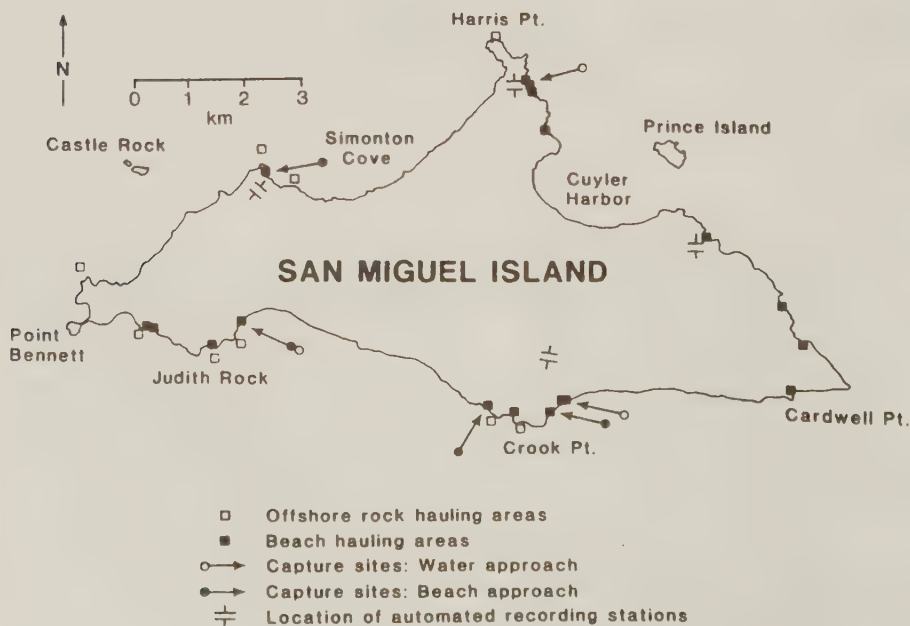


Figure 1. Harbor seal haul-out areas and capture sites on San Miguel Island.

SAN MIGUEL ISLAND, 1982

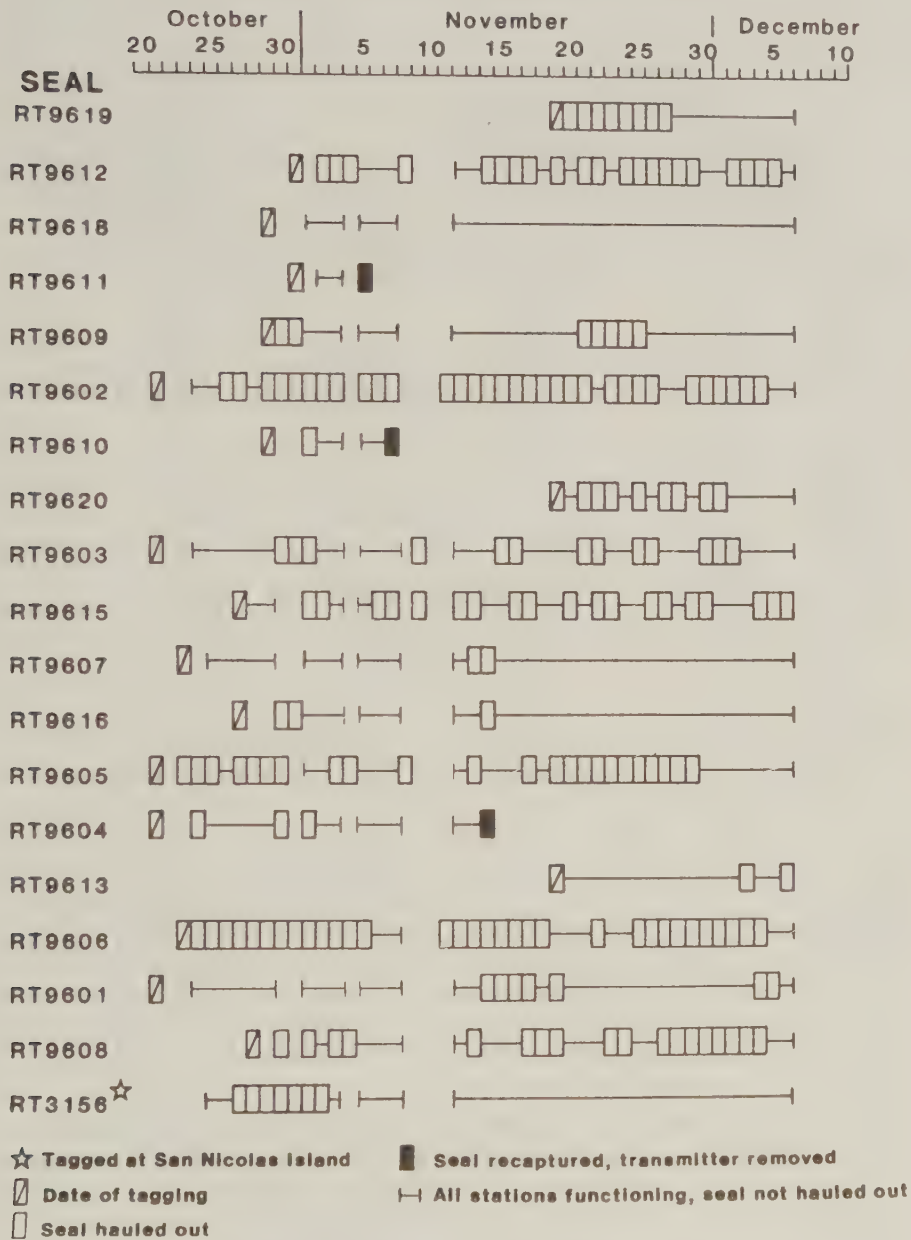


Figure 2. Daily presence of harbor seals on San Miguel Island in autumn, 1982.

Table 1. Location and elapsed time from capture of first resights of radio-tagged seals on San Miguel Island (OH = Otter Harbor, CK = Crook Point, TB = Tyler Bight, HS = Harris Point, HF = Hoffman Point).

Seal	Tagging site	Date tagged	Date of first resight	Location of first resight	Number of days after tagging before resighting
9601	CK	21 Oct	13 Nov	CK	22
9602	CK	21 Oct	26 Oct	CK	4
9603	CK	21 Oct	30 Oct	CK	8
9604	HS	21 Oct	24 Oct	HS	2
9605	HS	21 Oct	23 Oct	HS	1
9606	CK	22 Oct	23 Oct	CK	0
9607	TB	22 Oct	13 Nov	OH	21
9608	CK-TB	27 Oct	29 Oct	CK	1
9609	OH	29 Oct	29 Oct	HF	0
9610	OH	29 Oct	1 Nov	HF	2
9611	OH	31 Oct	5 Nov	HF	4
9612	OH	31 Oct	2 Nov	CK	1
9613	OH	19 Nov	3 Dec	OH	13
9615	OH	27 Oct	1 Nov	OH	4
9616	OH	27 Oct	30 Oct	OH	2
9618	CK	29 Oct	Not seen again		
9619	OH	19 Nov	20 Nov	OH	0
9620	OH	19 Nov	21 Nov	OH	1

them from concealed locations on the beach, or by swimming ashore from a motor vessel anchored 400 m to 500 m offshore from the haul-out site. We physically restrained each seal and then glued a VHF transmitter (6.5 cm long, 2 cm diameter, 50 g) to its dorsal pelage using a quick-setting epoxy. Each transmitter operated at a unique frequency between 164 and 165 MHz and radio signals were detected only when seals were hauled out. Transmission range was about 4 to 7 km and expected transmitter life was about four months.

We established automated recording stations at sites overlooking the major harbor seal haul-out areas at Hoffman Point, Harris Point, Otter Harbor and Crook Point (Fig. 1). Each station consisted of a programmable scanning receiver and a four element Yagi antenna connected to an Esterline Angus 20 channel event recorder. The entire system was powered by a 12-volt deep discharge marine battery. Except for a few days (see Figs. 2, 3) each haul-out site was monitored for the presence of radio-tagged seals automatically and continuously from 23 October 1982 through 6 December 1982. Each frequency in a receiver's memory was monitored for 32 sec each time that frequency was scanned. Because transmitter pulse rates varied from 40 to 80 pulses per min, scan intervals of 32 sec were sufficient to detect a seal if it was hauled out. Each frequency was

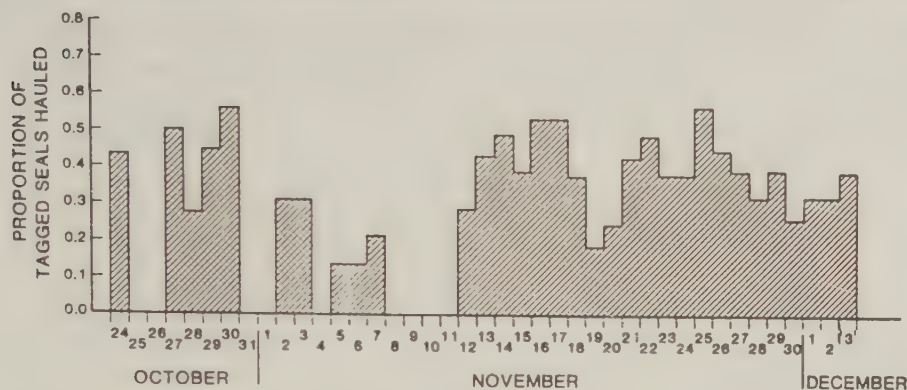


Figure 3. Proportion of radio-tagged seals hauled out at San Miguel Island by date (proportions are not presented for the dates 25, 26, 31 October, 1, 4, 8, 9, 10, 11 November because not all monitoring stations were operating on those dates).

scanned 6 to 15 times per h. depending on the number of frequencies being scanned. We placed a reference transmitter near each site to test for system malfunction.

We visited each site at least once every seven days to recharge batteries and service the event recorders. When we visited a haul-out site we searched for tagged seals for one to several hours to confirm that all transmitters were functioning.

On 11 November 1982 we surveyed, by air in a Cessna 337 Skymaster, all haul-out sites on San Miguel and Santa Rosa islands to document the number of seals ashore. We photographed seals that were hauled out at each site using a 35-mm camera (hand held) with a 75–210-mm telephoto lens and high speed color film. Counts of seals were made later from projected imagery. We determined the presence of radio-tagged seals at each site during those surveys using a portable scanning receiver attached to a four element Yagi antenna which was clamped to the aircraft's wing strut. On 1 December, we made an additional survey for radio-tagged seals at haul-out sites on Santa Rosa Island by circumnavigating the island in a 12-m motor vessel.

RESULTS

One of 18 radio-tagged seals was not resighted, either visually or by telemetry, during the study. Sixteen seals were resighted at least twice and 13 of those hauled out only at the sites where they were captured. Two seals used two sites and one seal used three, although each seal hauled out most often at its tagging site. All seals that hauled out at more than one site were first resighted at locations other than where they were tagged.

Three seals hauled out within one day of tagging whereas most others were absent for one to four days (Table 1). Two seals, which each used only one site, were absent from the island for more than 20 d after being tagged (Table 1, Fig. 2).

Table 2. Proportion of radio-tagged harbor seals hauled out during one-hour intervals

One-hour interval	Mean proportion of seals hauled out	Standard error
0000-0100	.13	.02
0100-0200	.13	.01
0200-0300	.14	.02
0300-0400	.14	.01
0400-0500	.14	.01
0500-0600	.14	.01
0600-0700		
(sunrise)	.14	.01
0700-0800	.14	.01
0800-0900	.15	.01
0900-1000	.16	.02
1000-1100	.16	.01
1100-1200	.17	.02
1200-1300	.18	.01
1300-1400	.19	.01
1400-1500	.19	.01
1500-1600	.18	.01
1600-1700	.16	.01
1700-1800		
(sunset)	.15	.02
1800-1900	.13	.02
1900-2000	.11	.02
2000-2100	.12	.02
2100-2200	.11	.01
2200-2300	.11	.02
2300-0000	.11	.01

Most seals (14 of 17) were hauled out on fewer than 51% of the days sampled (Fig. 3) and, on average, a seal hauled out on 37% (range 4% to 75%, SE = .02%) of the days. An average of 41% (range 14% to 60%, SE = .03%) of seals was hauled out each day. The percentage hauled out each day during any one-hour period was much smaller, varying from 11% to 19% with the greatest percentage ashore between 1300 and 1500 h (Table 2).

On average, about 11% to 14% of the radio-tagged seals were hauled out during one-hour periods at night (1800 to 0600 h) while about 14% to 19% were hauled out each hour during the day (0600-1800 h; Table 2). Seven of 17 radio-tagged seals were hauled out most often at night while six were hauled out most often during the day; there were no obvious preferences among the other four seals and the times of captures (between 1030 and 1730) did not explain the differences in haul-out behavior (Yochem 1987). Nearly as many haul-out bouts began at night (46%) as during the day (54%). Thirty-four percent of all haul-out bouts began between 0800 and 1300 h (Table 3). The median duration of all haul-out bouts was 6 h (range = 1 to 30 h); most (81%) were less than 12 h long and few (3%) were longer than 24 h (Fig. 4). The

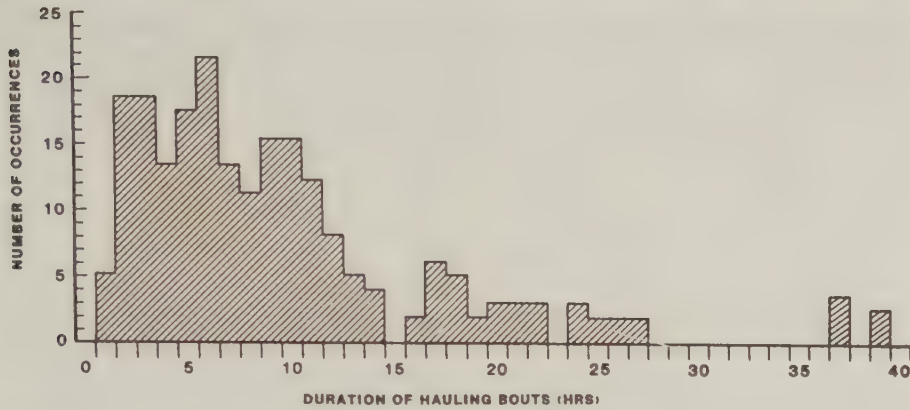


Figure 4. Frequency distribution of haul-out bout duration of harbor seals on San Miguel Island in autumn.

time at which a haul-out bout began had no apparent influence on its duration (Kruskal-Wallis one-way ANOVA, $P > .10$).

On 11 November between 1330 and 1400 h we counted 412 seals ashore on San Miguel Island. Using the telemetry data for seals hauled out during one-

Table 3. Haul-out bout onset time and duration.

Hour of onset of haul-out bout	Number of bouts	Median duration (hours)	Range (hours)
0000-0100	19	6	1-37
0100-0200	5	3	1-12
0200-0300	5	8	2-12
0300-0400	3	3	2-17
0400-0500	6	4	2-5
0500-0600	10	10	4-17
0600-0700	7	6	2-12
0700-0800	7	5	2-14
0800-0900	12	9.5	3-26
0900-1000	10	10	1-26
1000-1100	12	7	3-21
1100-1200	12	6	2-24
1200-1300	17	6	2-22
1300-1400	8	10	5-37
1400-1500	4	4	2-39
1500-1600	3	2	1-19
1600-1700	5	5	2-14
1700-1800	3	17	13-17
1800-1900	2	21	18-24
1900-2000	9	9	3-20
2000-2100	11	6	2-10
2100-2200	7	8	3-10
2200-2300	6	5	2-9
2300-0000	3	4	4-7

hour intervals (Table 2), we estimate that there were about 2,168 (95% confidence interval = 1,791 to 2,747) harbor seals using San Miguel Island then. Three of 14 radio-tagged seals were hauled out at the time of our survey; a modified Peterson mark-recapture model (Caughley 1977:142-143) yields a second estimate of 1,445 (SE = 643) seals.

DISCUSSION

Although we found that most seals were faithful to one haul-out site on San Miguel Island, we cannot exclude the possibility that some, or all, may have been hauled out at sites on other Channel Islands or on the California mainland when they were absent from San Miguel Island. We did not observe any radio-tagged seals at Santa Rosa Island (about 5.3 km east of San Miguel Island) during our aerial or boat surveys. However, one juvenile male that was tagged at San Nicolas Island (33°15'N, 119°30'W) on 8 May 1982, and that regularly used only one site when it hauled out there through early June (Stewart and Yochem 1983), was observed hauled out on San Miguel Island from 3 November through 7 November. This seal was seen again on San Nicolas Island in spring 1983 (Yochem and Stewart 1985). These observations suggest that some inter-seasonal movement of seals among the Southern California Channel Islands does occur. Pacific harbor seals in other areas have been reported to use two or more haul-out sites up to 192 km apart (*e.g.*, Divinyi 1971, Brown 1981, Pitcher and McAllister 1981, Brown and Mate 1983, Beach *et al.* 1985, Herder 1986, Yochem 1987). Most of the long distance movements were inter-seasonal or inter-annual whereas shorter distance movements between sites were apparently intra-seasonal. Except for those few observations, patterns of dispersal and migration (if migrations do occur) of Pacific harbor seals are unknown.

Our data suggest that disturbance during tagging may prompt some seals to relocate to new sites (Table 1). Of the seals that hauled out at more than one site, nearly all appeared at the second site immediately after being tagged. However, 12 of 17 seals did not move to other sites immediately after being tagged and 11 of those 12 continued to use only the sites at which they were tagged. Pitcher and McAllister (1981) reported that most seals radio-tagged at Tugidak Island, Alaska, were loyal to specific haul-out sites in summer. Those authors suggested, however, that capture, handling, and attachment of radio transmitters may have affected haul-out patterns or site use, or both, of some seals and may have accounted for the relocations of some seals to areas away from the tagging sites. Additional studies of identifiable undisturbed seals (*i.e.*, controls) are needed to test hypotheses about the effects of human disturbance on harbor seal haul-out patterns.

Stewart (1981) found that few harbor seals were ashore on San Miguel Island in early morning and late evening, suggesting that few, if any, seals were ashore at night. Our findings indicate, however, that significant numbers of seals are ashore at night, at least in autumn. Furthermore, some seals apparently prefer to haul out at night while others prefer to haul out during the day (Yochem

1987). These findings have obvious ramifications for determining absolute abundance of seals from counts made during the day.

Sullivan (1979) suggested that harbor seals in northern California spent an average of 44% of their "daily activity budgets" hauled out but he did not specify whether this was a seasonal or annual average. We found that when a seal hauled out on San Miguel Island in autumn it spent an average of about 8.9 h, or 37% (range 19% to 65%, SE = .03%), of each 24-h period ashore. The difference between harbor seals in northern California and on San Miguel island, if real, may be related to season of data collection, habitat influences on behavior, or the age and sex composition of our sample.

Our data on the proportion of seals ashore during one-hour intervals agree with earlier findings at San Miguel Island that the greatest number of seals is ashore in early afternoon (Stewart 1984). Stewart (1981) derived correction factors to estimate daily peak haul-out numbers from counts made at non-peak times of day. However, such derived estimates measure only relative abundance as seals do not haul out every day (Fig. 2) and all seals that do haul out on a particular day are not ashore during peak haul-out hours (Table 2).

Whether the data which we present on proportions of seals ashore each hour (Table 2) can be used to estimate absolute abundance from census data depends on at least two assumptions. The first is that the age and sex composition of our sample of radio-tagged seals accurately represented the age and sex composition of the population. This may not have been true as most (13) were young males. Furthermore, our observations at San Miguel and San Nicolas islands (*e.g.*, Yochem 1987) suggest that the sex and age composition of seals ashore varies seasonally.

The second assumption is that the proportion (daily or hourly) of the population which is hauled out is consistent among seasons and years. Data from San Nicolas Island suggest, however, that these proportions vary seasonally, and perhaps annually, in response to changes in the environment (Yochem and Stewart 1985, Yochem 1987).

Therefore, estimates of absolute abundance of harbor seals at the Southern California Channel Islands using proportional correction factors should be made cautiously until those assumptions can be adequately tested. Furthermore, applying such correction factors to harbor seal populations in other areas may be inappropriate without making preliminary studies of haul-out behavior there. Geographic variations in habitat, in prey availability, distribution and abundance and in levels of human disturbance are likely to influence harbor seal haul-out patterns and time budgets.

Clearly, additional studies are needed to test these assumptions and to refine methods of estimation of absolute abundance of harbor seals at the Southern California Channel Islands and in other parts of the species' range.

ACKNOWLEDGMENTS

We thank W. Ehorn and the staff of the Channel Islands National Park for their cooperation and assistance while this research was being conducted. We also thank G.

A. Antonelis, P. J. Gearin, J. Anderson, L. Pasaro, D. J. Seagars and D. M. Boone for field assistance, P. Howorth for his help in capturing seals and surveying Santa Rosa Island from his motor vessel *Solaris*, Channel Islands Aviation for their assistance in flying surveys and J. R. Jehl, Jr., J. A. Thomas, W. E. Evans, K. Pitcher and two anonymous referees for reviewing the manuscript. The radio receivers and transmitters were manufactured by Advanced Telemetry Systems, Bethel, Minnesota. Funding was provided by the National Marine Fisheries Service and Channel Islands Marine Sanctuary.

LITERATURE CITED

- BEACH, R. J., A. C. GEIGER, S. J. JEFFRIES, S. D. TREACY AND B. L. TROUTMAN. 1985. Marine mammals and their interactions with fisheries of the Columbia River and adjacent waters, 1980–1982. NWAFC Processed Report 85-04, NMFS, NWAFC, Seattle, WA. 316 pp.
- BROWN, R. F. 1981. Abundance, movements, and feeding habits of the harbor seal, *Phoca vitulina*, at Netarts Bay, Oregon. M.S. thesis, Oregon State University, Corvallis, OR. 69 pp.
- BROWN, R. F., AND B. R. MATE. 1983. Abundance, movements, and feeding habits of harbor seals, *Phoca vitulina*, at Netarts and Tillamook Bays, Oregon. U.S. Fishery Bulletin 81:291–301.
- CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York, NY. 234 pp.
- DIVINYI, C. A. 1971. Growth and movements of a known-age harbor seal. Journal of Mammalogy 52:824.
- HERDER, M. J. 1986. Seasonal movements and hauling site fidelity of harbor seals, *Phoca vitulina richardsi*, tagged at the Klamath River, California. M.A. thesis, Humboldt State University, Arcata, CA. 52 pp.
- PITCHER, K. W., AND D. C. McALLISTER. 1981. Movements and haulout behavior of radio-tagged harbor seals, *Phoca vitulina*. Canadian Field-Naturalist 95:292–297.
- STEWART, B. S. 1981. Seasonal abundance, distribution, and ecology of the harbor seal (*Phoca vitulina richardsi*) on San Miguel Island, California. M.S. thesis, San Diego State University, San Diego, CA. 66 pp.
- STEWART, B. S. 1984. Diurnal hauling patterns of harbor seals at San Miguel Island, California. Journal of Wildlife Management 48:1459–1461.
- STEWART, B. S., AND P. K. YOCHER. 1983. Radiotelemetry studies of hauling patterns, movements, and site fidelity of harbor seals (*Phoca vitulina richardsi*) at San Nicolas and San Miguel islands, California, 1982. HSWRI Technical Report 83-152. HMRI, 1700 South Shores Road, San Diego, CA 92109. 54 pp.
- STEWART, B. S., AND P. K. YOCHER. 1984. Seasonal abundance of pinnipeds at San Nicolas Island, California, 1980–1982. Bulletin of the Southern California Academy of Sciences 83:121–132.
- SULLIVAN, R. M. 1979. Behavior and ecology of harbor seals, *Phoca vitulina*, along the open coast of northern California. M.S. thesis, Humboldt State University, Arcata, CA. 115 pp.
- YOCHER, P. K. 1987. Haul-out patterns and site fidelity of harbor seals at San Nicolas and San Miguel islands, California. M.S. thesis, San Diego State University, San Diego, CA. 89 pp.
- YOCHER, P. K., AND B. S. STEWART. 1985. Radiotelemetry studies of hauling patterns, movements and site fidelity of harbor seals (*Phoca vitulina richardsi*) at San Nicolas Island, California, 1983. HMRI Technical Report 86-189. HMRI, 1700 South Shores Road, San Diego, CA 92109. 37 pp.

Received: October 6, 1986

Accepted: June 24, 1987

DAILY GROWTH INCREMENTS IN OTOLITHS
OF JUVENILE BLACK ROCKFISH,
SEBASTES MELANOPS: AN EVALUATION OF
AUTORADIOGRAPHY AS A NEW METHOD
OF VALIDATION

Investigations into the temporal periodicity of growth increment formation in otoliths of larval and juvenile fishes have produced conflicting accounts. Taubert and Coble (1977), Barkman (1978), Wild and Foreman (1980), and Campana and Neilson (1982), among others, have confirmed daily increment formation in otoliths from various species of larval and juvenile fishes. There have been a few studies, however, in which increment counts were not representative of actual age of the fish (Wild and Foreman 1980; Gefen 1982; Neilson and Geen 1982). Nondaily increment formation has been explained by the inclusion of subdaily rings in age estimates as well as by methodological errors in preparing and viewing the otoliths (Campana 1983a; Campana and Neilson 1985). Since size and age of fish, food limitations, and environmental conditions have been suggested to affect increment formation, validation is necessary in each study where fish age is estimated.

Several techniques have been used to validate daily growth increments in larval and juvenile fish otoliths. Fish of known age, raised from fertilization or birth under controlled laboratory conditions, provide the best material to determine frequency of increment formation (Taubert and Coble 1977; Barkman 1978; Tanaka et al. 1981; Miller and Storck 1982). For many species, however, rearing the larvae from birth through the juvenile stage is difficult or impossible. An alternate method of age validation introduces a chemical mark onto those calcified structures which exhibit periodic growth zones, such as otoliths, scales, and spines. The antibiotic oxytetracycline hydrochloride (OTC) has been used most successfully in this manner (Wild and Foreman 1980; Campana and Neilson 1982; Ralston and Miyamoto 1983; Dabrowski and Tsukamoto 1986). The OTC is taken up at the site of calcification and fluoresces bright yellow under ultraviolet light, compared with the blue autofluorescence of normal tissue. Most recently, stable strontium has been used to demonstrate daily increment formation in squid statoliths (Hurley et al. 1985) and in mass marking of coho salmon (Yamada et al. 1979). For some species, a time-mark may also be induced on the otolith by stress,

such as cold shock (Mugiya and Muramatsu 1982), or by simply bringing field-captured fish into the laboratory (Boehlert and Yoklavich 1985). Comparing increment counts with number of days following the time-mark accurately estimates frequency of occurrence of the growth increments. Our study evaluates the commonly used OTC and an alternate chemical, the radioisotope calcium-45, in terms of their success as time-markers to validate daily growth increment formation in the otoliths of juvenile black rockfish, *Sebastes melanops*.

Materials and Methods

Young-of-the-year black rockfish, *Sebastes melanops*, ranging from about 2 to 5 g wet body weight and 47 to 64 mm standard length (SL), were collected from a rocky, intertidal area 8 km south of Newport, OR, in July 1982 and from Yaquina Bay, OR, in July 1983. Fish were held in 200 L tanks under ambient water temperature conditions which fluctuated between 13° and 17°C; a ration of ground squid and shrimp was offered ad libitum and photoperiod was maintained at 13 h light and 11 h darkness. After at least 10 days of acclimation to laboratory conditions, fish were anesthetized with MS-222 and injected intramuscularly (midbody below dorsal fin) with a solution of either OTC or calcium-45. Fish continued to feed immediately following injection and handling.

Calcium-45

Fish were injected with a solution of low-calcium physiological saline and calcium-45 ($^{45}\text{CaCl}_2$ dissolved in HCl; New England Nuclear).¹ Through preliminary experiments, a dose of 0.1 μCi ^{45}Ca /g wet body weight proved to be optimum for isotope uptake and retention. Four fish each were sacrificed at 1, 4, 12, 24, 48, 72, 96, 120, 144, 168 hours and at subsequent 4-d intervals for 63 days following injection. Three fish were sacrificed after having maintained good health and growth for 1 year following injection. Four nonradioactive fish were sacrificed on the first day of the experiment and used as blanks or controls in determining activity levels of the injected fish.

At the time intervals specified above, fish were

anesthetized, blotted dry, measured (nearest mm, SL), and weighed (nearest 0.01 g). Both sagittal otoliths were removed from each fish, rinsed thoroughly in water to remove surface contamination of calcium-45, and stored dry for liquid scintillation counting (LSC) or autoradiography. One otolith from each fish, with the exception of the three 1-yr-olds, was weighed, dissolved in 0.1 mL concentrated HCl, diluted with 10 mL of Beckman Ready-solv EP liquid scintillation cocktail, and assayed for calcium-45 activity in a Beckman LS 8000 liquid scintillation counter. Activity was corrected for decay and quench and expressed as disintegrations per minute (DPM) per mg of sample. The perceived decrease in radioactivity due to the increase in weight of otolith over the experimental period was corrected using the following equation:

$$\text{Corrected activity} = \frac{\text{DPM}}{\text{mg tissue}_{t_f}} \times \frac{\text{weight tissue}_{t_f}}{\text{mean weight tissue}_{t_i}}$$

where t_f is time at sacrifice and t_i is time of experiment initiation. Mean weight of otolith at t_i was obtained from the 4 fish sacrificed prior to injection; since all fish were of similar length at the onset of experimentation, these 4 fish adequately represented size of injected fish.

Four otoliths from time interval 1 hour and two otoliths from each of intervals 4 and 12 hours and 1, 4, 11, 19, 39, 55, and 63 days were prepared for autoradiography. The right otolith of each pair was affixed to a microscope slide with histological mounting medium. The proximal surface of the otolith was ground with 600 grit carborundum paper on a rotating wheel until the focus was just visible and most of the curvature of the otolith was removed. The mounting medium was gently heated and the otolith was turned to expose the distal surface. Grinding was continued until most of the mounting medium was removed from the margins of the otolith. The external surface was polished using jeweler's rouge (3 μm) and the whole slide was immersed in an ultrasonic cleaner to remove all loose particles from the otolith surface. The resulting sagittal section was coated with Kodak NTB3 nuclear emulsion and exposed in a light-tight box for 8 days at 4°C. The autoradiographs were developed in Kodak D-19 developer for 2 minutes, fixed for 5 minutes in

¹References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

Kodak Fixer, rinsed for 20 minutes in distilled water, and viewed under transmitted light with a compound microscope at 400 $\times$ magnification to determine presence and location of exposed silver grains. Growth increments were enumerated from the time-mark to the otolith margin. In most of the otoliths, a check (or exceptionally dense band) was noted prior to the deposition of the radioactive mark. The location of this check, in terms of numbers of increments from the time-mark, was also determined.

Oxytetracycline

A stock solution was prepared using 25 mg OTC (Sigma Chemicals Co.) in 5 mL of physiological saline. Each fish received a dosage of 0.5 mg OTC or 0.1 mL of stock solution. This approximates the dosage reported by Mugiya and Muramatsu (1982) for goldfish and Weber and Ridgway (1962) for sockeye salmon smolts. Fish were sacrificed 21 days after injection, weighed and measured, and both sagittal otoliths were removed, cleaned, and stored dry in the dark.

A sagittal section of the right otolith was prepared as previously described. Sections were viewed at 160 $\times$ magnification, using a compound light microscope equipped with ultraviolet illumination. The fluorescent mark was located with an ocular marker. Increments were enumerated from this mark to the outer margins of the otolith using visible light.

Results and Discussion

Calcium-45

One hundred and three black rockfish were injected with the radioisotope, calcium-45; there were no mortalities during the 63-d postinjection sampling period. Over the course of the experiment, average fish length increased from 52.5 mm (SD = 1.29, N = 4) on day zero to 70.5 mm (SD = 8.23, N = 4) on day 63; average total body weight increased from 2.3 g (SD = 0.13, N = 4) to 8.10 g (SD = 2.60, N = 4).

LSC demonstrated that calcium-45 was taken up and retained in the sagittal otoliths of all fish. Incorporation of calcium-45 into the otolith occurred as early as 1 hour following injection, which was the initial sampling interval; mean activity at this time was 1,377 (SE = 329) DPM/mg otolith (Fig. 1). Similar activity values and uptake patterns of calcium-45, up to 72 hours

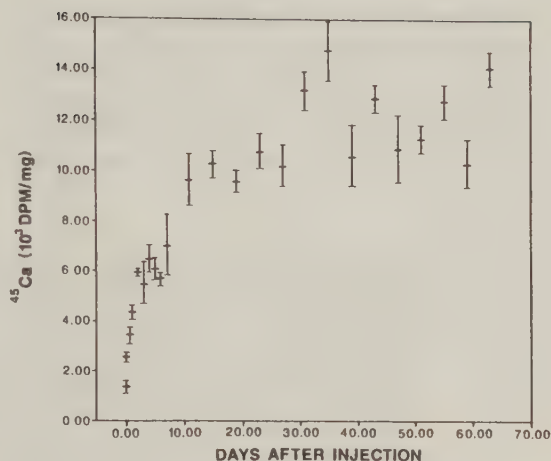


FIGURE 1.—Accumulation and retention of ^{45}Ca in the otolith of black rockfish. Mean activity and 1 SE are indicated. N = 2 to 4 fish per time interval.

postinjection, were observed in the otoliths of rainbow trout, although times of maximum incorporation and retention were not assessed over longer periods (Mugiya 1974). Radioactivity in the rockfish otoliths increased sharply for the first 15 days (up to an average of 10,279 DPM/mg, SE = 581), followed by a gradual increase to an apparent asymptote (Fig. 1). The rapid uptake and retention of calcium-45 in liver, muscle, and epidermis of *S. melanops*, and the gradual elimination of the isotope from these tissues (Yoklavich and Boehlert unpubl. data), could contribute to the increase in otolith activity over time; presumably, calcium-45 is transported from these tissues to the otolith via the blood (Mugiya 1974). The lack of decrease in activity in the otolith substantiates the findings of Ichii and Mugiya (1983) and Campana (1983b), which suggest that calcium deposited in otoliths of goldfish and stressed coho salmon, respectively, remains immobilized and is not resorbed. Although no data were presented, it had been suggested earlier by Pannella (1980) that resorption of calcium occurs in the otoliths of some tropical fish species, possibly invalidating ages based on increment counts. Our data show no evidence of resorption, lending support to the usefulness of increment counts in reliably estimating age.

Scattered exposed silver grains were evident along the interface of otolith section and mounting resin in the autoradiographs of otoliths from the earliest sampling periods (1 hour to 1 day), although positive association of the grains with a

distinct site of isotope incorporation into the otolith was not discernible. Since the radioactive mark was on the edge of the otoliths from these early sampling periods, it was more difficult to identify than the mark left on otoliths of fish sacrificed later in the experiment. Distinct bands of

silver grains, designating the site of isotope uptake, were evident in all but four otoliths sampled from day 4 through day 63 (Fig. 2). A less dense background of grains spanned 7 to 10 bands around the site of uptake; postinjection increment counts were made from the site of densest grain



FIGURE 2—Example of the silver grains produced by the autoradiograph of ^{45}Ca in the otolith of a 69 mm juvenile black rockfish. Arrow indicates band of densest grains; for scale, arrow = 35 μm . This photo is from the anterodorsal region of the otolith. Note the clear increments present on the left side of the figure, representing the increments distal to the time-mark.

accumulation to the edge of the otolith. The posterodorsal area of the sagittal sections showed the heaviest accumulation of the isotope and was also the easiest area in which to count increments. This observation is consistent with Irie (1960) and Mugiya (1974), who concluded that high calcium uptake occurred in the dorsal region, as well as in the anterior and posterior tips of otoliths; these are the regions of fastest otolith growth.

The number of growth increments from the band of densest accumulation of silver grains to the edge of the otolith section closely approximated the number of days the fish were held in the laboratory following injection (Table 1), thereby validating the occurrence of daily growth increments in these juvenile black rockfish. Validation of the frequency of growth increment formation, obtained from fish held under optimal growth conditions in the laboratory, and the apparent lack of otolith resorption, as demonstrated by the increasing retention of calcium-45 with time, suggest that daily increments on otoliths could provide accurate representation of age and growth for field-caught juvenile *Sebastes melanops*. Daily increments have recently been suggested to occur on otoliths of early larvae of *S. marinus* (Penny and Evans 1985). In previous work on juvenile *Sebastes*, growth increments had been counted but not validated (Moser and Ahlstrom 1978; Boehlert 1981). Our study is thus the first confirmation of daily increments on otoliths of juvenile *Sebastes*.

Checks, or exceptionally dense and dark bands

deposited as daily increments, were observed in otoliths from fish used in the calcium-45 experiments. One check preceded the radioactive time-mark and another check was associated with the time-mark itself. Ten growth increments were noted from the earliest check to the time-mark in each otolith (Table 1). Formations of checks in otoliths have been documented for many species, including coho salmon (Campana 1983b), goldfish (Mugiya and Muramatsu 1982), and several tropical species (Brothers et al. 1983). Such checks have been attributed to periods of physiological stress to the fish due to collection, migration, change in feeding or habitat, temperature, life history stages, or anything else that disrupts growth. In the present study, the time from fish collection to injection of the isotope marker was 10 days (Table 1). It seems clear that the observed checks were produced as a consequence of stress encountered during capture and transport to laboratory conditions and can be used as additional evidence of daily deposition of growth increments. If such checks are reliably produced, they may be better than chemical time-markers for validation studies such as these.

Oxytetracycline

The OTC was incorporated into the otoliths of each of the 15 fish injected and produced a distinct fluorescent band. The growth increments following injection of OTC, however, were less distinct on most of the otoliths and consequently all otoliths could not be used to validate daily increment formation. Weak increment definition following OTC incorporation in otoliths of larval spot and pinfish has been reported by Hettler (1984). Although Hettler suggested that the lack of distinct increments resulted from experimental stress, postinjection increments were clearly visible in otoliths from the juvenile rockfish which were injected with calcium-45 and held under laboratory conditions similar to the OTC experiments. Five of the rockfish otoliths did display clear growth bands following the fluorescent time-mark; enumeration of these increments is summarized in Table 1. These otoliths show the same results as those from calcium-45 treatments, demonstrating the daily periodicity of growth increment formation in juvenile black rockfish. It is unclear, however, why 67% of the otoliths failed to produce prominent daily increments after OTC incorporation.

The fluorescent OTC mark was more intense

TABLE 1.—Age validation using otoliths from black rockfish marked with calcium-45 or oxytetracycline. Number of days from capture to injection is compared with number of growth increments from capture check to time-mark; number of days from injection to sacrifice is compared with number of increments from time-mark to margin of otolith.

Treatment/ sample size	Number of days from		Mean number increments from	
	Capture- injection	Injection- sacrifice	Check- mark	Mark- margin
⁴⁵ Ca/4	10	0.04	10	10
/2	10	0.17	10	10
/2	10	0.5	10	10
/2	10	1	10	10
/1	10	4	10	4
/1	10	11	10	11
/1	10	19	10	19
/2	10	39	10	36
/1	10	55	10	55
/2	10	63	10	63
OTC /5		21		21

¹Scattered silver grains associated with margin.

and easier to identify than the exposed silver grains in the autoradiographs of most otoliths. OTC is less hazardous to handle in the laboratory and can be detected in the otolith for much longer periods than calcium-45. The OTC was still visible in the otolith at least 3 years following injection and has in fact been used in studies for mass-marking of fish for identification purposes, where time at liberty may be even longer (Tsukamoto 1985). The activity of calcium-45 was evident in autoradiographs of a few otoliths which were developed 2 years following injection; amount of activity depends upon the effective half-life of the isotope (164 days for calcium-45) and the initial amount of activity in the tissue. An autoradiograph of a transverse section through the otolith of one of the fish injected and held for 1 year revealed a discontinuous band of very faint, exposed silver grains, dispersed primarily over the internal and dorsal areas of the otolith. Association of the isotope with an annular band was not observed. Autoradiographs are difficult to produce, expensive, and time consuming. On the other hand, OTC is simply observed in the otolith section under ultraviolet light. Our recommendations for validating the daily formation of growth increments in juvenile rockfishes are 1) the use of OTC, if growth increments can be routinely identified following injection, or 2) stress marks, which are induced either when transferring fish from the field to laboratory or by subjecting fish to abrupt environmental changes. Where this type of induced stress is not appropriate, as in environmentally controlled laboratory studies, and OTC marking is unsuccessful, marks could reliably be produced with the calcium-45 technique described in this paper.

Acknowledgments

We thank S. L. Boehlert for generously offering her expertise in preparation of the autoradiographs. We also appreciate the helpful comments of S. E. Campana, S. Ralston, and an anonymous reviewer on earlier drafts of this manuscript. This research was supported by NOAA, National Marine Fisheries Service, Northwest and Alaska Fisheries Center, Seattle, WA, through contract 81-ABC-00192-PR6.

Literature Cited

- BARKMAN, R. C.
1978. The use of otolith growth rings to age young Atlantic silversides, *Menidia menidia*. Trans. Am. Fish. Soc. 107:790-793.
- BOEHLERT, G. W.
1981. The effects of photoperiod and temperature on laboratory growth of juvenile *Sebastes diploproa* and a comparison with growth in the field. Fish. Bull., U.S. 79:789-794.
- BOEHLERT, G. W., AND M. M. YOKLAVICH.
1985. Larval and juvenile growth of sablefish, *Anoplopoma fimbria*, as determined from otolith increments. Fish. Bull., U.S. 83:475-481.
- BROTHERS, E. B., D. MCB. WILLIAMS, AND P. F. SALE.
1983. Length of larval life in twelve families of fishes at "One Tree Lagoon", Great Barrier Reef, Australia. Mar. Biol. 76:319-324.
- CAMPANA, S. E.
1983a. Feeding periodicity and the production of daily growth increments in otoliths of steelhead trout (*Salmo gairdneri*) and starry flounder (*Platichthys stellatus*). Can. J. Zool. 61:1591-1597.
1983b. Calcium deposition and otolith check formation during periods of stress in coho salmon, *Oncorhynchus kisutch*. Comp. Biochem. Physiol. 75A:215-220.
- CAMPANA, S. E., AND J. D. NEILSON.
1982. Daily growth increments in otoliths of starry flounder (*Platichthys stellatus*) and the influence of some environmental variables in their production. Can. J. Fish. Aquat. Sci. 39:937-942.
1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42:1014-1032.
- DABROWSKI, K., AND K. TSUKAMOTO.
1986. Tetracycline tagging in coregonid embryos and larvae. J. Fish Biol. 29:691-698.
- GEFFEN, A. J.
1982. Otolith ring deposition in relation to growth rate in herring (*Clupea harengus*) and turbot (*Scophthalmus maximus*) larvae. Mar. Biol. 71:317-326.
- HETTLER, W. F.
1984. Marking otoliths by immersion of marine fish larvae in tetracycline. Trans. Am. Fish. Soc. 113:370-373.
- HURLEY, G. V., P. H. ODENSE, R. K. O'DOR, AND E. G. DAWE.
1985. Strontium labelling for verifying daily growth increments in the statolith of the short-finned squid (*Illex illecebrosus*). Can. J. Fish. Aquat. Sci. 42:380-383.
- ICHII, T., AND Y. MUGIYA.
1983. Comparative aspects of calcium dynamics in calcified tissues in the goldfish *Carassius auratus*. Bull. Jpn. Soc. Sci. Fish. 49:1039-1044.
- IRIE, T.
1960. The growth of the fish otolith. J. Fac. Fish. Anim. Husb. Hiroshima Univ. 3:203-229.
- MILLER, S. J., AND T. STORCK.
1982. Daily growth rings in otoliths of young-of-the-year largemouth bass. Trans. Am. Fish. Soc. 111:527-530.
- MOSER, H. G., AND E. H. AHLSTROM.
1978. Larvae and pelagic juveniles of blackgill rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and Baja California. J. Fish. Res. Board Can. 35:981-996.
- MUGIYA, Y.
1974. Calcium-45 behavior at the level of the otolithic organs of rainbow trout. Bull. Jpn. Soc. Sci. Fish. 40:457-463.
1982. Time-marking methods for scanning electron microscopy in goldfish otoliths. Bull. Jpn. Soc. Sci. Fish.

- 48:1225-1232.
- NEILSON, J. D., AND G. H. GEEN.
1982. Otoliths of chinook salmon (*Oncorhynchus tshawytscha*): daily growth increments and factors influencing their production. *Can. J. Fish. Aquat. Sci.* 39:1340-1347.
- PANNELLA, G.
1980. Growth patterns in fish sagittae. In D. C. Rhoads and R. A. Lutz (editors), *Skeletal growth of aquatic organisms: biological records of environmental change*, p. 519-560. Plenum Press, N.Y.
- PENNY, R. W., AND G. T. EVANS.
1985. Growth histories of larval redfish (*Sebastes* spp.) on an offshore Atlantic fishing bank determined by otolith increment analysis. *Can. J. Fish. Aquat. Sci.* 42:1452-1464.
- RALSTON, S., AND G. T. MIYAMOTO.
1983. Analyzing the width of daily otolith increments to age the Hawaiian snapper, *Pristipomoides filamentosus*. *Fish. Bull., U.S.* 81:523-535.
- TANAKA, K., Y. MUGIYA, AND J. YAMADA.
1981. Effects of photoperiod and feeding on daily growth patterns in otoliths of juvenile *Tilapia nilotica*. *Fish. Bull., U.S.* 79:459-466.
- TAUBERT, B. D., AND D. W. COBLE.
1977. Daily rings in otoliths of three species of *Lepomis* and *Tilapia mossambica*. *J. Fish. Res. Board Can.* 34:332-340.
- TSUKAMOTO, K.
1985. Mass-marking of ayu eggs and larvae by tetracycline-tagging of otoliths. *Bull. Jpn. Soc. Sci. Fish.* 51:903-911.
- WEBER, D. D., AND G. J. RIDGWAY.
1962. The deposition of tetracycline drugs in bones and scales of fish and its possible use for marking. *Prog. Fish-Cult.* 150-155.
- WILD, A., AND T. J. FOREMAN.
1980. The relationship between otolith increments and time for yellowfin and skipjack tuna marked with tetracycline. *Inter-Am. Trop. Tuna Comm. Bull.* 17:507-541.
- YAMADA, S. B., T. J. MULLIGAN, AND S. J. FAIRCHILD.
1979. Strontium marking of hatchery-reared coho salmon (*Oncorhynchus kisutch*, Walbaum). *J. Fish. Biol.* 14:267-275.

Mary M. Yoklavich

Mark O. Hatfield Marine Science Center
Oregon State University
Newport, OR 97365
Present address: Northwest and Alaska Fisheries Center
National Marine Fisheries Service, NOAA
7600 Sand Point Way NE, BIN C15700
Seattle, WA 98115

George W. Boehlert

Southwest Fisheries Center Honolulu
Laboratory
National Marine Fisheries Service, NOAA
2570 Dole St.
Honolulu, HI 96822-2396

